



Abstracts - Speeches

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Plant and ecosystem water relations - an introduction

Christian Körner, University of Basel

On a global scale, potential biome distribution is defined by a few key environmental variables tied to temperature and moisture. Deviations of actual vegetation from what 'should' grow in a certain area are nearly exhaustively explained by disturbance regimes, both natural and anthropogenic. For instance, today forests grow on only about 42% of the land area suitable for tree growth. Hence a large fraction of global land cover is not in equilibrium with the current climate. Changes in water regimes may thus affect ecosystems depending on how large that discrepancy between potential and actual land cover is.

Irrespective of such ecosystem states, soil water shortage acts upon plants in a sequence of steps of action, different from what is often assumed. Soil moisture deficits first affect microbial activity and thus, availability but also mobility of nutrients (upper soil layers). As moisture shortage progresses, plants can not maintain the turgor needed for cell expansion and tissue formation, hence meristematic activity declines and gets interrupted. Finally, wilting will affect photosynthetic CO₂ uptake, which is the last process in this chain reaction to shut down. As structural demand for carbon products declines, ongoing photosynthesis may fill storage pools, but eventually the decline in structural growth will negatively feedback on photosynthesis by end product inhibition. In that sense, growth or sink activity control plant carbon assimilation.

Plants differ in their sensitivity to drought because they differ both, in rooting depth as well as water use. Hence, the ultimate consequence of changing water availability will be a change in species abundance and even presence. It is these community changes, including stand density adjustments, which will determine the long term outcome of exposure to a new water regime. 'Long-term' may be 5-10 years in grassland and 100-200 years in forests. A result from such successional community processes is that the physiological controls conventionally considered of forefront significance decline in importance. Both, empirical work and models need to account for the causal hierarchy of impacts of water shortage on plant growth and allow for structural adjustments of land cover, the ultimate determinant of plant water relations at the individual plant level. Once the 'right' species are at the 'right' place, and once LAI is adjusted, physiological controls of water relations at leaf level become of minor significance.

Potential decoupling of plant-microbial processes by precipitation change.

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The close coupling of microbial nutrient mineralization and plant nutrient uptake processes contributes to the efficiency of nutrient recycling in temperate forest ecosystems. This coupling is due in part to the influence of plants on microbial activity, via the timing and chemistry of carbon inputs to the soil system. Inputs of C to the rhizosphere and the gradual metabolism of plant litter and soil organic matter should support fairly consistent microbial activity and hence nutrient mineralization throughout the growing season. The timing of nutrient mineralization is further coupled to the timing of plant nutrient demand by seasonal changes in the chemistry of mineralized substrates. This general synchrony between plant nutrient demand and microbial release of nutrients is hypothesized to be sensitive to changes in precipitation in two related ways. First, decoupling between microbial and plant processes may result from fine-scale heterogeneity within soil particles when low water availability restricts movement of nutrients and labile C. Second, decoupling between microbial release and plant uptake of nutrients may occur temporally. Accumulation of C substrates while soils are dry is predicted to cause a flush of microbial activity upon re-wetting. This intense period of microbial activity is likely to enhance nutrient leaching, but also may promote transfer of nutrients to microbial and organic pools or, in the case of phosphorus, to biologically unavailable mineral pools. Evaluation of these predictions requires direct comparison of rates of response to rain events by decomposer microorganisms, extracellular enzyme activities, and activities of roots and mycorrhizae. Alteration of nutrient dynamics via altered timing and spatial patterns of plant-microbe interactions may not have immediate effects on forest productivity or C storage. However, elucidation of the plant-microbe responses to precipitation change should prove useful for understanding longer-term changes in nutrient recycling and storage in forest ecosystems.

Bioclimate driven distributions

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The precipitation regions of the Earth are determined by the macro-scale structure of the atmosphere, the locations and dynamics of the major high and low pressure systems and their relationships to the spatial and temporal dynamics of sea surface temperatures in the different ocean basins. This large-scale atmospheric structure will not change; however, the hydrologic cycle is expected to accelerate, producing more intense storms and unusual patterns of both spatial and temporal variability. The current boundaries between wet and dry regions are the regions of the greatest uncertainty with respect to changes in precipitation regimes.

Annual precipitation, its seasonality and variability clearly determine biome distributions and disturbance regimes. The seasonality of precipitation, especially in temperate zones, determines the degree of deep soil moisture recharge, which can be critical to supply the transpiration demands of woody species during the growing season. The vertical distribution of soil moisture throughout the growing season both affects and is affected by the vertical distribution of roots of different plant life forms and the competition between those lifeforms. Thus, summer dry regions behave quite differently from summer wet regions with respect to overstory-understory competition as well as the frequency and intensity of wildfire. Year to year and decade to decade variability of the seasonal precipitation affects the disturbance regime and can control the distribution of biomes. Changes in ocean circulation will affect these spatial and temporal patterns of variability. Drought, fire and other disturbances will resonate with climate variability and trends, as will the internal inertia of ecosystems.

Ecosystems tend to grow until their leaf area will just barely use the available soil moisture; however, periodic disturbances can keep them below this leaf area carrying capacity. Walter's 2-layer competition theory works well, but positive feedbacks at ecotones can enhance their 'sharpness', the importance of horizontal interactions and plant lifeform distinctions. That is, if a wet forested region slowly dries to a point where the canopy opens, then the light going to the forest floor enhances grass growth, which removes more water from the trees, further opening the canopy. The more grass, the greater is the risk of fire, which can open the canopy even further. A key uncertainty in future responses of ecosystems to elevated CO₂ and global warming is the degree to which CO₂ will confer increased water use efficiency, potentially forestalling the drying response of vegetation to increased temperatures. Thus, elevated CO₂ could have a profound effect on ecotones and biomes

Variability, at all timescales will change and will affect all stages of the life cycle. For example, the establishment niche is critical for both the spread and persistence of vegetation, but currently is not included in most models.

European Precipitation Reconstructions AD 1500 - 2000

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An attempt is presented to reconstruct precipitation for European land areas (30°W to 40°E / 30°N

to 71°N; given on a 0.5°x0.5° resolved grid) covering the period 1500-1900 together with gridded reanalysis from 1901-2000. Principal Component Regression techniques were applied to develop this dataset. A large variety of long instrumental precipitation series, precipitation indices based on documentary evidence and natural proxies (tree-ring chronologies, ice cores, corals and a speleothem) that are sensitive to precipitation signals were used as predictors. Transfer functions were derived over the 1901-1983 calibration period and applied to 1500-1900 in order to reconstruct the large-scale precipitation fields over Europe.

The performance (quality estimation based on unresolved variance within the calibration period) of the reconstructions varies over centuries, seasons and space. Highest reconstructive skill was found for winter over central Europe and the Iberian Peninsula.

Precipitation variability over the last half millennium reveals both large interannual and decadal fluctuations (see Figure 1). Applying running correlations, we found major non-stationarities in the relation between large-scale circulation and regional precipitation. For several periods during the last 500 years, we identified key atmospheric modes for southern Spain/northern Morocco and central Europe as representations of two precipitation regimes.

Globally, there have been significant precipitation trends in many regions. Especially the middle and high latitudes, precipitation has systematically increased over the 20th century. However, there was no overall trend in European precipitation over the last 500 years although there were various trends on interdecadal timescales (Figure 1).

Due to its high spatial and temporal resolution, this precipitation dataset allows detailed studies of regional precipitation variability for all seasons, impact studies on different time and space scales, comparisons with high-resolution climate models as well as analysis of connections with regional temperature reconstructions.

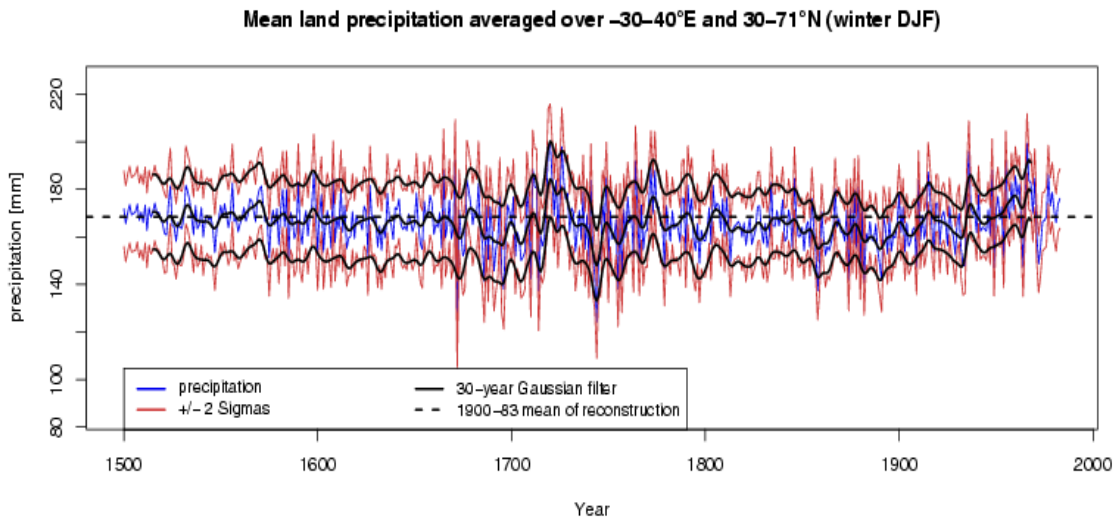


Figure 1: Spatially averaged time series and uncertainty estimates of the European winter (December-February) precipitation reconstruction. To the original reconstruction

(blue curve) and its uncertainties (red curves) a 30-year-Gauss-filter is applied to stress the interdecadal fluctuations.

Future Global Change Projections

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Scientific understanding of anthropogenic global climate change has advanced notably in recent years, and led to commensurate developments of mitigation strategies. International discussions on mitigation are primarily founded on the present understanding of observed current and future projected global-scale change, and are aimed at identifying actions that can be taken by multiple nations or regions. In contrast, adaptation decisions and actions tend to be more of a local and regional scale issue, and are limited by the measure of confidence in the projected changes over smaller spatial scales. It is at regional scales that the need for credible information on probable climate change and the associated uncertainties is the greatest.

In view of this clear need, much effort has been expended in recent years on developing regional projections. Global Climate Models (GCMs) only provide information at the scale they are able to resolve, at best, but important aspects of model performance in many regions of the World rely on details related to the treatment of processes at the unresolved scales. Therefore, alternative methods have been developed to derive detailed regional information at finer scales than that resolved by GCMs. Through nested Regional Climate Models (RCMs) or empirical downscaling, these developments have generated new ways to assess important regional processes central to climate change. However, to date, much of the work remains at the level of methodological development. Downscaled climate change projections that are tailored to the needs of the impacts community, and which are based on projections across different forcing GCMs, are only starting to become more available.

In the present paper, some of the most recent advances in addressing regional climate change issues are highlighted based on multiple global model simulations. In addition an illustrative example is shown, that documents that current global model simulations cannot be used as the only tool to deduce credible regional information about the plausible future climate and associated changes in hydrological extremes.

Session 2 Effects of precipitation alone

Historical data

Steven W. Leavitt, University of Arizona, US

Tree Rings and Water

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Historical and remote sensing data on the impacts of precipitation changes on Mediterranean ecosystem functioning.

Observations and Space-for-time substitution

Philip Ciais, CEA Saclay, FR

Recent changes in the European carbon balance detected from atmospheric observations

Dimitris Sarris, University of Patras, GR

Precipitation decline in the eastern Mediterranean and its impacts on trees growth and ground water utilization

Manipulation experiments

Alan K. Knapp, Colorado State University, US

Responses of a mesic grassland to the manipulation of rainfall quantity and pattern

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Throughfall Displacement Experiment (TDE). Understanding Mechanisms of Eastern Deciduous Forest Ecosystem Adjustments to Altered Precipitation

Franco Miglietta, IBIMET-CNR, IT

The EU-MIND Project: Mediterranean ecosystems and drought

Daniel C. Nepstad, Woods Hole Research Center, US

The interaction of drought, fire regime, and carbon fluxes from the Amazon: field experiments and model results.

Claus Beier, Risoe National Laboratory, DK

VULCAN - Drought experiments across European shrublands in DK, UK, NL, SP, IT, HU

Osvaldo Sala, Brown University, US

Lags in the Response of Primary Production to Changes in Water Availability

Michael Loik, University of California, Santa Cruz, US

Snow Depth Forcing of Seasonal Photosynthesis Following an El Niño Winter for a High-Elevation Desert.

Tree Rings and Water

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The imprint of environmental conditions on cambial growth produces interannual tree-ring-width variability that forms the basis of dendrochronological dating. In turn, the variation of ring width and other wood properties (e.g., density, anatomy and isotopic composition) can be used to infer the past variability of these environmental parameters, including moisture and its various manifestations such as rainfall, drought, relative humidity, and streamflow. These wood properties record variations in moisture that may have important if not catastrophic effects on ecosystems, and offer chronologies of these conditions/events hundreds if not thousands of years in length. In addition to the above parameters, the age structure of wooded ecosystems as derived from dendrochronology provides insight into temporal variability of moisture. Even the occurrence of sequence of fires at the stand scale to regional scale has been demonstrated to be strongly linked to wetness/dryness teleconnections from ENSO in the U.S. Southwest. Stable carbon and oxygen isotopic analysis offers additional opportunity to supplement water-related environmental information from the other tree-ring sources, perhaps even providing information for different time windows or for different parameters.

Historical and remote sensing data on the impacts of precipitation changes on Mediterranean ecosystem functioning.

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We presented biological responses to precipitation change taking as pilot field site the Montseny Mountains (Barcelona) which constitute an ecotonic area between the wet temperate and the Mediterranean biome. We presented the species contrasts in phenological responses to precipitation changes, and the spatial and temporal contrasts in growth responses of beech trees from the higher tree-line to the lower forest limit, and from several decades ago to nowadays. We then passed from phenotypic responses to genotypic responses and microgeographic differentiation of individuals (adaptation). Finally, we presented data on beech migration resulting from amelioration in the higher altitudinal-latitude ranges and replacements in the lower altitudinal-latitude ranges, increasingly arid in the last decades. We also presented interactions of the precipitation change effects with those of other components of global change with an example of fragmentation of the beech forest, also in the Montseny Mountains. As a result of the contrasting responses, significant changes in ecosystem structure and functioning are expected. We have already observed many of these changes in experimental studies that, for example, show biodiversity losses in response to rainfall exclusion in Mediterranean forests and shrublands. Finally, we presented the use of the remote sensing indices NDVI, PRI and WI to assess water status of ecosystems.

Recent changes in the European carbon balance detected from atmospheric observations

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The European continent is a net source of CO₂ to the atmosphere. Emissions of fossil fuel CO₂ amount to 1.82 ± 0.18 PgC y⁻¹ on average in the 1990's [Marland *et al.*, 2006] while sinks in European ecosystems are in the range 0.11 ± 0.28 PgC y⁻¹ [Janssens *et al.*, 2003]. This gives a mean European carbon balance of 1.71 ± 0.33 PgC y⁻¹. Note that the uncertainty on the terrestrial uptake is larger than the one on fossil fuel emissions at the continental scale. The atmosphere is a fast, but incomplete mixer of the surface fluxes. Hence, time and space gradients in atmospheric CO₂ concentrations in the European air shed can be used to constrain the large scale carbon balance of the continent and its variations. Obtaining quantitative estimates of sources and sinks of CO₂ from concentration measurements requires a numerical model of atmospheric transport. Finding the sources which optimally fit to the observations within their errors is called inverse modelling [Gurney *et al.*, 2002; Rödenbeck *et al.*, 2003].

Our goal here is not to carry out an inversion of the European carbon balance, but rather to analyze long-term trends in the carbon budget of the continent directly from concentration measurements. We analyzed the CO₂ concentration long term time series from three long term observatories, Mace-Head (Ireland), Schauinsland (South-Western Germany), Hegyhatsall (Western Hungary) and Alert (Canada). The Mace Head station is located on the western coast of Ireland. Atmospheric CO₂ concentration is measured there each hour on a continuous basis since 1992. Atmospheric CO₂ varies in response to sources and sinks and to synoptic air mass transport. This station receives alternatively maritime air masses from the Atlantic Ocean, or continental air masses exposed to sources over Europe or Ireland. Marine air masses are

generally well mixed, and carry systematically lower concentrations than continental air masses [Bousquet *et al.*, 1997]. Given the fact that the air-sea fluxes of CO₂ are an order of magnitude smaller than vegetation fluxes and that the marine boundary layer has negligible diurnal changes, CO₂ recorded at Mace-Head in the marine sector also shows little temporal variations (typically < 0.5 ppm). Selection of CO₂ at Mace-Head in the marine sector only (strong winds from the Atlantic ocean, small hourly standard deviation of CO₂) defines a marine baseline seasonal value of CO₂ [Bousquet *et al.*, 1997]. This baseline can be used as a reference for stations located in the interior of the continent.

We analyzed atmospheric CO₂ records from two continental stations, Schauinsland and Hegyhatsall. The Schauinsland station is on the top of a 1200 mountain in the Black forest region. It is the longest CO₂ observatory in Europe, with a 30 years long record [Levin *et al.*, 1995]. In winter times, vertical mixing is reduced (except during frontal passages) and the mountain top often lies above the mixed boundary layer. This causes a decoupling between nearby emissions and CO₂ recorded at the station. In contrast, in summer, convection develops systematically in the late morning, delivering air recently exposed to surface emissions up to the mountain top. Since anthropogenic emissions in the vicinity of Schauinsland are important and ubiquitous (Rhin valley), the data selection performed at this station consists in retaining preferentially episodes of strong winds in the early morning, when air masses have a regional origin and contain minimum contamination by nearby pollution [Schmidt *et al.*, 2003]. The Hegyhatsall station is a tall tower in the western plains of Hungary. Sampling on the top (115 m) of a TV transmission tower puts the measurements outside the surface layer, and during daytime, within the well-mixed convective boundary layer [Haszpra *et al.*, 2001]. CO₂ records during daytime are regionally representative of a large area, and were shown to be coherent at scales of at least 100 Km [Haszpra, 1999]. We retained only mid-afternoon CO₂ values in this analysis, to avoid contamination by local soil and plant respiration at night.

Hourly or daily CO₂ concentration data (not shown) generally exhibit a great variability linked to synoptic transport and weather patterns. Assuming that such a weather-related variability does not change on the long term, and acts as a 'noise' superimposed on slower seasonal and interannual variations, the data were filtered in the time domain using a low-pass filter [Thoning *et al.*, 1989] to retain only CO₂ concentration changes on time scales greater than approx. 80 days. The CO₂ time series are given in Figure 1. We observe that the CO₂ seasonal cycle increases in amplitude when going inland from Mace-Head to Hegyhatsall. In winter, the continental stations indicate higher CO₂ values than Mace-Head, as implied by soil respiration and fossil fuel emissions. The winter difference to the marine reference is positive, and it is higher at Hegyhatsall (12.1 ppm) than at Schauinsland (1.6 ppm). Thus, in winter,

advection acts to transport CO₂ from the continent to the ocean, while a positive CO₂ difference gets maintained by permanent regional emissions. In contrast, in summer, CO₂ inside the continent lies hardly below the marine reference curve. Vertical mixing is more vigorous in summer than in winter, and dilutes the surface fluxes into a thicker mixed layer, contributing to render the summertime negative CO₂ gradient between land and ocean smaller in absolute value than the wintertime positive gradient. There are also different phases of the seasonal cycle of CO₂ between continental stations and Mace-Head.

Figure 2 (top) shows the deseasonalized CO₂ trends obtained by subtracting at each site a least-square fit of 4 harmonics to the seasonal cycle. On average (1995-2005), the difference between Schauinsland and Mace-Head is of 1.6 ± 0.5 ppm, and of 4.3 ± 0.8 ppm between Hegyhatsall and Mace-Head. The standard deviation reflects interannual variability in transport and in fluxes. The mean positive value reflects the source of CO₂ due to the sum of fossil fuel emissions and terrestrial sinks. Interestingly, the five recent years show an increasing difference between inland stations and Mace-Head. In fact, the CO₂ difference to the marine reference of Mace-Head moved up from 1.5 to 1.9 ppm (+26%) at Schauinsland, and 3.8 to 4.8 ppm (+ 28%) at Hegyhatsall between the late 1990's (1995-2000) and the early 2000's (2000-2005). The difference was especially high in 2003 and 2005 when droughts occurred in summer, in South Western Europe only during 2005 and in Western and Central Europe in 2003, with extreme heat in Western temperate regions (ECMWF, operational analyses)

Scaling the long term mean estimate of the European carbon balance of 1.71 PgC y^{-1} obtained above by the ratio of the CO₂ difference, we infer that European CO₂ emissions increased on average by 0.46 PgC y^{-1} (+27%) between the 2000s and the late 1990's. It is unlikely that fossil fuel emissions increases have caused this change. Fossil fuel emission inventories in Western Europe have only increased by 0.05 PgC between the mid 1990's and the early 2000's [Marland *et al.*, 2006]. Thus, one can infer that over the past five years, the European terrestrial ecosystems have been losing more (or absorbing less) CO₂ than before. This yields to revise the European terrestrial carbon sink estimated by Janssens *et al.* of 0.11 ± 0.2 for the 1990's to a source of 0.35 ± 0.2 during the early 2000's. Such a rough and ready estimate of changes in the European carbon balance awaits further analysis by vegetation models and inverse modelling.

Fig. 1. Long term atmospheric CO₂ records of interest for the European carbon balance, during the past 14 years (1992-2005). Hourly in situ records are been filtered in the time domain to remove variations on time scales shorter than approx. two months. The data are from Mace-Head in the marine sector only (blue), Schauinsland with data filtered from local contaminations (orange), Hegyhatsall with data only from day-time conditions (red) and Alert (green)

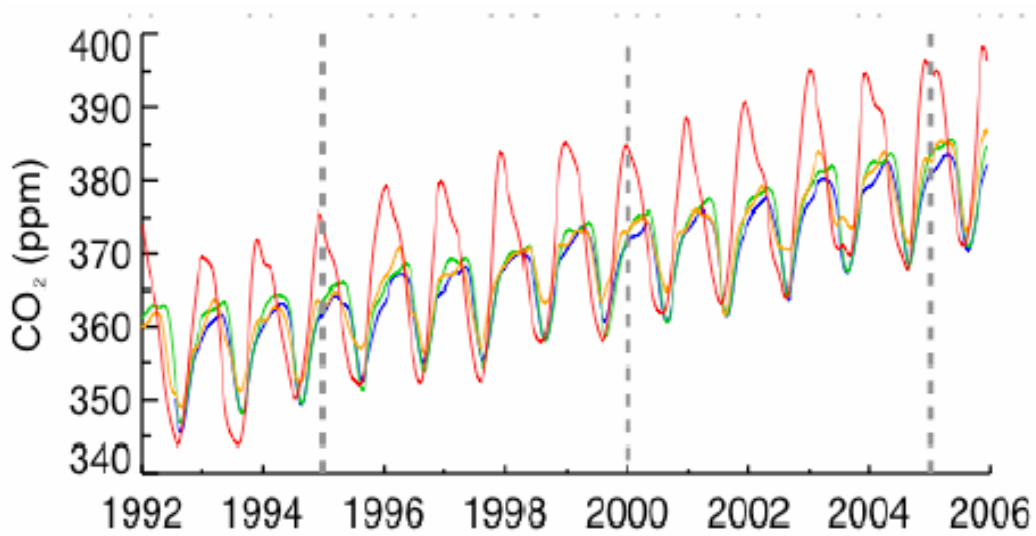
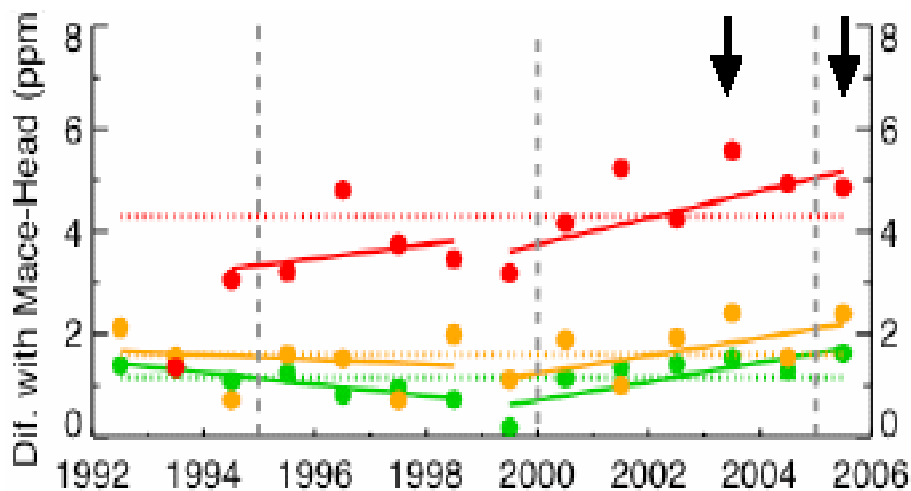


Fig. 2. Recent trends in the CO₂ difference between continental sites (data selection in text) and the reference curve of Mace-Head in the marine sector. Each dot is the yearly mean CO₂ value at each site (Orange = Schauinsland, Red = Hegysatsall, Green = Alert). The colored dotted lines represent the long term mean CO₂ difference during the full period years 1992-2005. The two arrows mark years 2003 and 2005, during which extensive drought prevailed in temperate and central Europe and in south-western Europe, respectively.



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Precipitation decline in the eastern Mediterranean and its impacts on trees growth and ground water utilization

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We present evidence of a recent drying in the eastern Mediterranean, based on weather and tree-ring data for four islands, Samos, Zakynthos, Skiros and Crete, covering an area of ca. 550 km from east to west and ca. 450 km from north to south. Rainfall declined rapidly after the late 1970s following trends for the entire Mediterranean, which was associated with reduced tree-ring width in *Pinus brutia*. The most recent decline led to the lowest annual radial stem increment of the last 100 years and was found to be ENSO associated. An in depth investigation for the island of Samos of the eastern Aegean Sea revealed that as precipitation decreased trees became increasingly dependent on longer periods of water supply and were possibly utilizing moisture from deeper soil horizons stored during rainfall of several previous years. Correlation analysis suggests that the buffering capacity of deep soil moisture exceeded five years of precipitation prior to and including the year of tree-ring formation. Such long-term integration periods of tree growth responses to precipitation have not been reported before. They may reflect a tree-rooting pattern adapted to cope with even a few dry years. In late summer 2000, moisture reserves became exhausted however and a substantial fraction of low altitude pines died, including some 80-year-old trees, which underlines the exceptional extent this trend had reached. Our findings provide empirical support for IPCC model predictions of reduced precipitation over the Mediterranean, its eastern basin in particular.

Keywords: Drought, precipitation, tree-rings, Pinus, ENSO, climate change, Greece, Mediterranean

Responses of a mesic grassland to the manipulation of rainfall quantity and pattern

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Climatic variability is an inherent feature of grassland biomes. Large fluctuations in temperatures combined with precipitation regimes characterized by floods and severe drought occur at both an interannual and seasonal scales. Global climate models and emerging data indicate that extremes in precipitation regimes are increasing worldwide coupled with increases in temperature. Thus, variability in spatial and temporal patterns of water availability in grasslands, as directly influenced by altered precipitation patterns and indirectly by increased temperatures, will likely increase in the future. Experiments at the Konza Prairie (USA) are designed to experimentally manipulate rainfall amount and temporal patterns (amount and timing of individual rainfall events) to assess soil, plant, community and ecosystem responses to this projected climate change.

Two long-term experiments in undisturbed mesic grassland in eastern Kansas are ongoing: a 14-yr water supplementation study and a 7-yr experiment in which growing season rainfall patterns (variability) have been manipulated without altering total amounts. Both experiments are fully replicated with the irrigation study designed to alleviate seasonal water limitation, and the rainfall variability experiment designed to increase rainfall event size concurrent with lengthening periods between events by 50%, but with no change in total growing season rainfall amount.

Water availability has limited aboveground net primary production (ANPP) all but 2 years of the irrigation study, even in this mesic grassland. Within-season increases in precipitation extremes characterized by fewer, larger rainfall events with longer intervening dry periods, has led to a suite of responses including reduced ANPP and soil respiration and shifts in plant community structure. Plant community structure has also begun to shift in the irrigation study, altering the relationship between precipitation and ANPP. A more recent addition of a heating treatment nested within the RaMPs study has shifted plant community structure even more significantly.

**Throughfall Displacement Experiment (TDE)
Understanding Mechanisms of Eastern Deciduous Forest Ecosystem Adjustments to
Altered Precipitation**

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Changes in regional precipitation expected to result from increasing global temperatures are predicted to have a major effect on the composition, structure and productivity of forest ecosystems. From 1993 through 2005, a catchment-scale chronic manipulation of precipitation inputs to an upland oak forest was conducted. This long-term, experiment allowed the evaluation of instantaneous and cumulative responses to scenarios of chronically reduced (-33%) or increased (+33%) annual rainfall. Interannual variation in amount and distribution of growing season precipitation produced late-season soil water deficits in about half of the years, which were exacerbated by the TDE manipulations. Wet treatments delayed the onset of droughts and exacerbated dormant season percolation and associated soil leaching.

Leaf photosynthesis, conductance, and were reduced by up to 50%, and dormant season carbohydrate storage pools was shown to drop below 10% following severe droughts. Measurements of stand-level water use also indicated that late-season water use on the dry plot could be reduced 17 to 29% compared to ambient controls. Nevertheless, evidence for the translation of these physiological responses to current-year changes in tree basal area growth was not obtained. Through 13 years of manipulation, observations of growth of trees greater than 20 cm diameter showed no significant cumulative effect of chronic rainfall change. This resilience results from a disconnect between early summer tree growth phenology and late-season drought.

Contrary to an initial hypothesis, annual leaf production on the dry plot exceeded that of the wet and ambient treatment plots by ~100 g m⁻² y⁻¹. This difference is interpreted as the result of excessive leaching of beneficial plant elements (e.g., Ca and Mg but not N) from the ambient and wet plots. Long-term observations of seedling populations show increases for up-slope wet and ambient plots, but decreases in the dry plots over the 13-y manipulation. Reduced seedling survival associated with drier precipitation regimes will have important implications for the long-term diversity of eastern forest systems.

The TDE data archive was used to evaluate multiple, stand-level models for their ability to capture intra- and inter-annual components of the water and carbon cycle for an upland, oak-dominated forest of eastern Tennessee. The comparisons showed good agreement among model predictions for water cycle fluxes, but considerable disagreement for predicted carbon fluxes. The predictive capacity of all models deteriorated under drought conditions suggesting that further work is needed to evaluate and improve ecosystem model performance under unusual conditions, such as drought, that are a common focus of environmental change

discussions. The relative importance of multiple environmental change drivers was further evaluated using a site-specific model with inputs based on lessons-learned from a variety of environmental change studies. This analysis revealed that elevated CO₂ and temperature would be the dominant drivers of change for similar eastern deciduous forests of the future.

Project web site: <http://tde.ornl.gov> ; Program web site: <http://per.ornl.gov>

TDE Related Literature:

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The EU-MIND Project: Mediterranean ecosystems and drought

Franco Miglietta [Institute of Biometeorology – National Research Council (IBIMET-CNR) Via Caproni, 8 50145 Firenze, Italy]

Will Mediterranean terrestrial ecosystems be affected by the expected changes in climate? And how much? Two simple questions that are the basis of the research we made in the MIND project. Over three consecutive years, 10 European laboratories have created four experimental infrastructures and have developed original research to acquire new information on the response of Mediterranean ecosystems to changes in drought severity and frequency. Mediterranean-type climate occur roughly between 30° and 40° latitude and is unique in that the wet season coincides with the low sun or winter period with dry summers. The Mediterranean region is considered one of the most vulnerable in Europe to climate change because of its sensitivity to drought and rising temperatures. Countries bordering the Mediterranean are supposed to suffer an increased risk of severe water shortages, forest fires, lost of agricultural land. "The Mediterranean appeared most vulnerable to global change" concluded the ATEAM (Advanced Terrestrial Ecosystem Analysis and Modelling Project) coordinated by the PIK (Potsdam Institute of Climate Impact Research). In the region, water scarcity will likely be aggravated by greater demand for water for irrigation and tourism. Although droughts are a normal summer phenomenon – especially in the Mediterranean area where the ecosystem services are well adapted – a change in its emergence pattern may cause a water scarcity over a certain period of time or within a certain region.

The MIND project aimed to assess ecosystem vulnerability to drought at various locations in Southern Europe, thus providing valuable information on the potential consequences of climate change at the regional scale. The key objectives were i) to investigate the potential effects of increasing drought on Mediterranean terrestrial ecosystems at the process, ecosystem and regional scales and ii) to assess ecosystem vulnerability in response to changes in rainfall patterns. To attain such objectives, a coordinated network of experimental study sites has been created in Portugal, Spain, France and Italy where ecosystem manipulations have been made to alter the amount of water that is available to the vegetation. The most up-to-date methods of environmental physiology, micrometeorology and remote sensing have been used to elucidate the mechanisms that regulate the response of the vegetation to changes in water availability and this information is providing the basis for the implementation and validation of simulation models capable of predicting the drought response of Mediterranean terrestrial ecosystems, and their vulnerability, on a larger scale. The results that have been obtained are continuing to elucidate how water availability affects plant ecophysiological responses, the dynamics of soil carbon and the overall exchange of mass and energy between the land and the atmosphere. Accordingly, the experimental data that have been obtained at the different MIND sites, together with methods, indices and models that have been tested and validated across those different sites are providing unprecedented information to acquire substantial knowledge on ecosystem functioning, resilience and tolerance to drought stress.

This presentation focuses on a few important results that have been obtained in the MIND project that include, for a forest dominated by *Arbutus unedo*, in Italy, the observed increase in leaf photosynthesis in response to irrigation, and a significant change in the allocation of resources to vegetative and reproductive growth with a positive effect on flowering caused by imposed drought. Changes in litterfall in response to drought/irrigation have been documented in Portugal (*Quercus suber*, montado ecosystem) and to a lesser extent in Italy. Interesting effects of drought/irrigation on soil respiration have been observed in Portugal, Spain and Italy. Respiration pulses (the so-called Birch effect) caused by irrigation during the summer months have been compensated by reduced soil respiration in response to autumnal rains. An observation that is consistent across the experimental sites. A significant reduction of the emission of volatile organic compounds (VOCs) has been observed in France on a holm oak stand (*Quercus ilex*) subjected to artificial drought. Those preliminary results/observations represent only a small fraction of the information gathered by the MIND project.

The interaction of drought, fire regime, and carbon fluxes from the Amazon: field experiments and model results.

Daniel Nepstad, Woods Hole Research Center, Instituto de Pesquisa Ambiental da Amazonia

Several processes may be increasing the frequency and severity of drought in the Amazon basin, but little is known of how this trend will influence Amazon ecosystems. We report on a recently-completed, six-year experiment of partial throughfall exclusion in a one-hectare rainforest plot, experimental fires, and Basin-wide modeling. These results indicate that both positive and negative feedbacks are at work in the Amazon drought-fire-carbon interaction. Partial throughfall exclusion was associated with two surprising responses: (a) an increase in the mortality of large canopy trees (from 2% yr⁻¹ in the control to 6% yr⁻¹ in the treatment plot) greater than that for small, understory trees, and (b) a decrease of stemwood increment while leaf litterfall and, perhaps, belowground production changed very little. Tree mortality reduced live aboveground biomass by approximately 11% during the five-year treatment period. Experimental fires found that fire spread rate and forest floor ignition were positively related to forest interior VPD, and negatively related to forest canopy height and leaf area index. Both drought and fire therefore increase forest flammability. Land use also interacts with drought and fire by (a) decreasing evapotranspiration and increasing atmospheric aerosol loading, thereby inhibiting rainfall, (b) by thinning the canopy (in the case of selective logging), (c) by providing sources of ignition (in the case of ranching and swidden agriculture) and (d) by providing sources of highly flammable herbs and forbs. When these experimental results are incorporated into an ecosystem model for the Amazon, we find that drought alone can cause fluxes of carbon to the atmosphere on the scale of nearly one billion tons per year, of the total forest tree carbon pool of 120 billion tons.

VULCAN - Drought experiments across European shrublands in DK, UK, NL, SP, IT, HU

Claus Beier, Bridget Emmett, Albert Tietema, Josep Penuelas, Inger K. Schmidt and Olevi Kull.

VULCAN investigates the impacts of warming (+1 °C) and drought (1-2 months) on ecosystem functioning in European shrublands by experimental manipulations of 6 shrubland ecosystems in Europe (Denmark, the Netherlands, United Kingdom, Spain, Italy and Hungary). This design combines a field scale experimental approach with the gradiental or “space for time” approach. The effects of the treatments on plants, soils, fauna and soil water processes are studied.

Results for the impact of drought shows:

Plants

- Plant growth is often reduced or limited during the drought
- Biodiversity (Species numbers are reduced and relative abundance of plant species is changed)

Soil:

- Soil mineralization (C and N) is reduced at medium and low water conditions and is increased at high water contents
- Long term soil structure change (water retention and rewetting changed)
- Long term increase in N leaching at high N status.

Conclusions or statements

- Sites at wet conditions may be just as strongly affected by drought as semidry and dry sites.
- Repeated drought events may have long term consequences for soils

Lags in the Response of Primary Production to Changes in Water Availability

Oswaldo E. Sala, Brown University

Long-term time series of aboveground primary production and annual precipitation suggest the existence of time lags in the response of primary production to increases in water availability. Lags seemed evident in North American shortgrass steppe and in the Patagonian steppe. Years with the lowest precipitation corresponded with years with the lowest production. However, in the following years, when precipitation was average or above average, production was still much lower than the mean and lower than what it would have been expected based on annual precipitation.

We reported on a manipulative experiment in the Patagonian steppe designed to test the existence of the lags, evaluate whether the intensity of previous drought controlled the magnitude of the lags, and finally evaluate the ecological mechanisms responsible of the lags. We had a factorial experimental design where we reduced incoming precipitation by 20, 50, and 80% for 2 years. Drought treatments were followed in the third year by control or experimentally enhanced precipitation. We used passive rainout shelters to establish the drought treatments. We were able to experimentally reproduce the lags suggested in the long term observations and to establish causality. Moreover, we found that the magnitude of the lags was proportional to the intensity of previous year drought.

Our results suggest two mechanisms that may result in time lags in production through structural or biogeochemical constraints. During drought the density of individuals was drastically reduced in a way that was proportional to the intensity of the drought. After the drought, the low density of individuals may constrain the ability of the ecosystem to fully utilize the water resources available in an average or above-average year. During the drought years, plant growth and immobilization were impaired but nitrogen mineralization was not. Consequently, soil nitrate accumulated in drought treatments. We suggest that accumulation of nitrate, which is a very labile form of N, may make the ecosystem susceptible to losses via deep percolation when rainfall resumes.

Snow Depth Forcing of Seasonal Photosynthesis Following an El Niño Winter for a High-Elevation Desert.

Loik ME, AB Griffith, and H Alpert.

General circulation model scenarios of future precipitation patterns are highly uncertain regarding patterns of snow depth and snow melt timing. Because snowfall provides the majority of annual soil water recharge in many western high-elevation North American ecosystems, this study tested hypotheses about the linkages of snow depth to soil water content and physiological performance of deeply-rooted shrubs at the ecotone between the Great Basin Desert shrub-steppe and Sierra Nevada conifer forest. Snow depth was manipulated using eight long-term snow fences near Mammoth Lakes, Mono County, California, USA. Snow depth, soil moisture content, water potential, photosynthetic gas exchange, and leaf area index changes were measured for *Artemisia tridentata* and *Purshia tridentata* in response to increased and decreased snow depth in the spring and summer following typical (2003 – 2004) and El Niño (2004 – 2005) snowfall years. Snow depth on increased-depth (“+snow”) plots was about twice that of ambient-depth plots in both years, and about 2.2 times of that for decreased-depth (“-snow”) plots. Soil water content on + snow plots was double that on ambient and – snow plots in the El Niño year, and approximately 5% greater following the typical snowfall year. Photosynthetic gas exchange differed across snow depth treatments for both species in June 2004 (following the typical snowfall winter of 2003 – 2004). Following the El Niño winter, plant water potential did not differ across snow depth treatments until early September, and photosynthetic CO₂ assimilation increased from May to September for all treatments. We conclude that there is a threshold level of sensitivity of soil and plant water relations and photosynthesis to snow depth such that plant physiological responses to microscale differences in snow depth are reduced in high-snowfall El Niño years, whereas snow depth effects are more pronounced in typical-snowfall years.

Session 3 Interactions of precipitation with other global change drivers

Historical data

Jeffrey S. Dukes, University of Massachusetts, US

Interactions among climate change drivers - lessons from the past: Results from the Jasper Ridge Global Change Experiment

Observations and Interannual variability

Stanley D. Smith, University of Nevada, Las Vegas, US

Interactions of Precipitation and Elevated CO₂: El Niño/Drought Cycles in the Mojave Desert

Sebastian Leuzinger, Universität Basel, CH

Results from the Swiss Canopy Crane FACE experiment: CO₂ x water interactions

Paul Dijkstra, Northern Arizona University, US

Interacting effects of precipitation, CO₂ concentration, temperature and N-deposition on N-cycling in a California annual grassland.

Manipulation experiments

Aimee Classen, The University of Tennessee, US

OCCAM project

Bridget Emmett, Centre for Ecology & Hydrology, Bangor, UK

Talk and Challenge : Impacts of drought and interactions with grazing and nitrogen

Rebecca Sherry, University of Oklahoma, US

Lag Effects of Climatic Anomaly on Ecosystem Processes in Oklahoma

David Briske, Texas A&M University, US

Texas Warming and Rainfall Manipulation (T-WaRM) Project: Growth Form Contrasts in Oak Savanna

Sune Linder, Swedish University of Agricultural Sciences, SE

Long-term manipulation of water and nutrients in Norway spruce stands

Interactions among climate change drivers - lessons from the past: Results from the Jasper Ridge Global Change Experiment

Jeffrey S. Dukes¹

(summarizing work of many other JRGCE-affiliated researchers, including Nona R. Chiariello³, Elsa E. Cleland³, Lisa A. Moore², M. Rebecca Shaw², Erika S. Zavaleta⁵, Harold A. Mooney³, and Christopher B. Field²)

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While many studies have examined ecosystem responses to individual global environmental changes, relatively few have examined responses to multiple changes. Because many global changes are happening simultaneously, our ability to predict ecosystem functioning depends on an understanding of responses to interacting changes. Since 1997, the Jasper Ridge Global Change Experiment (JRGCE) has examined the response of California grasslands to elevated CO₂, warming, increased precipitation, and nitrate deposition. Over the first five years of the experiment, biomass production of the grassland responded most strongly to supplemental nitrate deposition, with an average increase of 26%. Root and shoot production did not respond to elevated CO₂ or modest warming. Supplemental precipitation led to increases in shoot production and offsetting decreases in root production. Interactions among the main treatments were rare. Over these five years, root:shoot ratios were reduced by nitrate deposition (due to increases in shoot growth), and by increased precipitation (due to decreases in root growth). In plots dominated by annual plants, responses to precipitation were most positive in plots receiving supplemental nitrate. Across all years and treatments in annual-dominated plots, responses to nitrate increased with increasing precipitation.

Over the first three years of the experiment, increased precipitation increased the diversity, abundance, and production of forbs, and the diversity of grasses in the JRGCE. Changes in species richness in the main treatments can be used to accurately predict species richness shifts in the combined treatments, suggesting treatment effects on richness are additive.

Elevated CO₂ and warming shifted first flowering dates of species most strongly, and precipitation had no effect. Elevated CO₂ accelerated flowering of annual forbs, but slowed flowering of annual grasses. Warming accelerated flowering of most species.

Related publications, and greater detail on the experimental design and treatments, are available at: <http://globalecology.stanford.edu/DGE/Dukes/JRGCE/home.html>

Interactions of Precipitation and Elevated CO₂: El Niño/Drought Cycles in the Mojave Desert

Stanley D. Smith

Department of Biological Sciences

University of Nevada, Las Vegas (USA)

The Nevada Desert FACE Facility (https://www.unlv.edu/Climate_Change_Research/) is a multi-investigator project in which the responses of an intact desert ecosystem to elevated [CO₂] is being studied. Our lab is examining aboveground production responses to elevated [CO₂] in concert with the highly episodic inter-annual rainfall patterns that typify the arid Mojave Desert. Over an eight-year period (1998–2005), the site has experienced two El Niño's (a strong event in 1998 and a weaker event in 2005) bracketing a six-year drought cycle. Contrary to early predictions, we have found that primary production is significantly stimulated only in wet years, and the accumulated eight-year increase in aboveground perennial biomass at elevated [CO₂] was almost completely accounted for by production increases in the strong El Niño year of 1998. Likewise, annual plant production in response to elevated [CO₂] primarily increased in 1998, with apparent negative effects on the seed bank in intervening drought years. Our results from the first eight years of treatment in this desert ecosystem thus suggest that elevated [CO₂] may result in even more episodic inter-annual productivity cycles than occur at present. We propose, however, that if precipitation significantly increases in this arid region, as some GCM's have predicted, we should see potentially dramatic increases in production of both perennials and annuals at elevated [CO₂] in the future.

Results from the Swiss Canopy Crane FACE experiment: CO₂ x water interactions

S. Leuzinger and Ch. Körner

Institute of Botany, University of Basel, Basel, SWITZERLAND

In summer 2003, central Europe faced a centennial drought period with less than half of the precipitation and 2-4 degrees higher monthly average temperatures than the long-term mean. We monitored leaf water potential, sap flow and phenology of 5 common deciduous tree species to reveal the impact of such extreme climate conditions. All data were collected in a diverse temperate forest near Basel (Switzerland) at the site of the Swiss Canopy Crane, where parts of the trees are subjected to elevated CO₂ (540 ppm). We found that predawn leaf water potential dropped from -0.9 Mpa after the first eight weeks of drought in July to approximately -1.5 Mpa during the driest period in mid August. Relative sap flow varied greatly between species, with daily peaks remaining relatively constant over the whole period in *Quercus petraea* and decreasing 20 to 40% of the early summer maximum in *Carpinus betulus* and *Fagus sylvatica*. Stomatal conductance and net rate of photosynthesis decreased dramatically in mid August. Phenological data showed less basal stem area increase and prolonged leaf longevity compared to data from previous years. We measured higher rates of net photosynthesis and less negative predawn leaf water potential in CO₂-treated trees in 2003. Data from the following years suggest that tree transpiration reaches saturation at greater vapour pressure deficit and ca. 16 % less water is transpired in CO₂-enriched trees across all weather conditions and species. Water is extracted more slowly under CO₂-enriched trees at first, but a reverse effect is seen as drought proceeds. Overall, these data suggest that the extreme drought did not cause severe water stress. Initial benefits for the water status of trees growing under elevated CO₂ may be mitigated by time-dependent feedback effects.

Interacting affects of precipitation, CO₂ concentration, temperature and N-deposition on N-cycling in a California annual grassland.

Paul Dijkstra, Jamie R. Brown, Joey S. Blankinship, Graham Hymus, Noel P. Gurwick, Hugh A.L. Henry, Chris B. Field and Bruce A. Hungate

Nitrogen availability is a major determinant of ecosystem productivity. Knowledge of how N-cycling is affected by (interacting) global change factors is central to predicting future ecosystem productivity and C-sequestration potentials. Few studies have looked at the effects of climate change on N-cycling; even fewer studies have focused on the response to combinations of global change factors. Here we will present results from measurements done in a California annual grassland (Jasper Ridge Global Change Experiment). We studied the effects of precipitation, atmospheric CO₂ concentration, temperature and N-deposition (in all combinations) on inorganic N availability, gross nitrification and NO₃ consumption rates, and net N₂O production. Measurements were done before germination, at mid-vegetative stage and at the time of peak biomass. Main conclusions drawn from these measurements are 1) precipitation affects inorganic N concentrations and process rates only in interaction with other global change factors, 2) the effects of global change factors were most evident before germination, and declined during the growing season, and 3) most significant effects of precipitation, CO₂ concentration and temperature were found under increased N-deposition, indicating that N-limitation restricted the response to other climate change factors in this ecosystem.

Old-field Community Climate and Atmospheric Manipulation (OCCAM)

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Global change effects on ecosystems have been examined primarily in single factor and single species experiments. But many ecosystems are complex and global change encompasses factors such as increasing atmospheric concentrations of carbon dioxide, rising temperature, and altered precipitation. We constructed an ecosystem with seven plant species typical of old-field ecosystems, including C3 and C4 grasses, forbs, and legumes to investigate the interactive effects of elevated CO₂, temperature, and water on ecosystem productivity and function. In this presentation, we used two data sets, total aboveground biomass and NDVI, to make three main points: 1) Patterns of response in our ecosystem change significantly from year to year, 2) Complex ecosystems lend themselves to complex results making it difficult to interpret patterns, and 3) Background climate may mediate treatment effects over time. For example, in 2004 total aboveground biomass was significantly greater in wet treatments than in dry treatments ($p = 0.04$). This pattern was significant in 2005 ($p = 0.004$), but in addition there were significant interactions between biomass and temperature ($p = 0.04$) and biomass and CO₂ ($p = 0.02$). Plant species responded differently to treatments in 2004 and in 2005. Clover and Solidago responded significantly to treatments in 2004, while Lespedeza and Dactylis responded significantly to treatments in 2005. These results demonstrate that patterns of response can change from year to year and that species can respond differently to treatments. NDVI tells a similar story. In 2004, dry plots had lower NDVI than wet plots ($p = 0.004$) and warm plots had lower NDVI than cool plots ($p = 0.02$). However in 2005, when there was a dry spell resulting in a 20% decrease in growing season soil moisture at our field site, interactions emerged. Dry plots still had lower NDVI than wet plots ($p = 0.01$), but dry and warm plots had lower NDVI than wet and warm plots ($p = 0.06$). A water by temperature interaction may emerge when the plots are drier overall, suggesting that background climate may influence experimental results. Taken together, these results suggest that single factor experiments many overlook complex interactions among environmental drivers.

Talk and Challenge : Impacts of drought and interactions with grazing and nitrogen

BA Emmett¹, A Sowerby¹, Z Frogbrook¹ and B Reynolds¹, I Schmidt, A Tietema, and C Beier

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Predicted changes in rainfall precipitation patterns will occur concurrently with changes in both land use/management and air pollution. Here the potential interaction between increased frequency of summer drought and changes in (i) grazing pressure and (ii) increased nitrogen deposition are discussed:

(i) Many studies have indicated the effect of grazing pressure on rates of litter build-up, soil organic matter content, rooting patterns, and vegetation structure although direction and magnitude of change differs between system types. In Wales, 12 million sheep currently graze large areas of grassland which dominate the landscape. Here, data will be shown from a field experiment which also indicate a doubling in rainfall infiltration rates when sheep grazing pressure is reduced from 1 sheep to 0.5 sheep/ha for 10 years due to changes in soil physical structure. These effects however are most pronounced in organic soils emphasising the importance soil type in determining the response of key soil processes to changes in rainfall pattern.

(ii) Nitrogen deposition is increasing or predicted to remain elevated in many areas. Interactions with drought are likely due to changes in root:shoot ratios, phenology, productivity, herbivory and vegetation composition which will all affect either the use or storage of water . One example from the EU CLIMOOR study demonstrates the importance of pre-conditioning of ecosystems by N deposition with respect to response of nitrate leaching to warming. A second example, show both the importance of the indirect effects of drought on N availability and that of soil type: Repeated summer drought resulted in increased decomposition of surface peat layers and N availability resulting in both a stimulation of plant productivity and soil respiration at the cold/wet Climoor site in Wales contrasting with declines at warmer/drier Climoor sites.

Key messages are:

- Changes in soil physical structure due to grazing pressure or changes in land use/management may have significant effects on impacts of changing rainfall frequency

- Effect of drought and their interaction with nitrogen and grazing are all heavily influenced by soil type

- Cold/wet soils may be some of the most sensitive to changes in rainfall frequency due to feedbacks on N availability

- Experiments across climatic gradients are very powerful in providing 3 levels of information (i) treatment data, (ii) between year data and (iii) across gradient data.

Lag Effects of Climatic Anomaly on Ecosystem Processes in Oklahoma

R. A. Sherry and Y. Luo

Climate change is predicted to increase frequency of extreme weather events and anomalously warm, wet, or dry years. This study was designed to examine the effects of an anomalously warm and wet year on all aspects of the tallgrass prairie ecosystem during the treatment year and in the following year. Some of the results are reported here. Radiant infrared heaters warmed plots an average of 4.1°C, with greater warming during summer. A 2x natural precipitation treatment increased soil moisture by an average of 10.1%. Warming and 2x precipitation increased soil CO₂ efflux additively. After the end of treatments, soil moisture in the upper most layer of soil in warmed plots did not recharge to the level of control plots for 2 months. In the lowest soil level examined, soil water recharge in warmed plots was not completed in 10 months. Above-ground biomass nearly doubled in warmed plots during spring of the treatment year. As summer drought set in, biomass in 2x precipitation plots over took that in warmed plots, and warmed plots had the least biomass in fall of that year. Warmed plots also had less biomass into summer of the next year due to the delay in soil moisture recharge. C₄ grasses increased in warmed plots during the treatment year as well as in the following fall, a 9 month carry-over effect.

Texas Warming and Rainfall Manipulation (T-WaRM) Project:

Growth Form Contrasts in Oak Savanna

David D. Briske, Mark G. Tjoelker and Astrid Volder
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Southern oak savanna may be especially sensitive to climate change because of intensified summer drought and contrasting photosynthetic pathways and leaf habit among dominant species. *Quercus stellata* (post oak) is the dominant deciduous tree, *Schizachyrium scoparium* (little bluestem) is the dominant C₄ grass, and *Juniperus virginiana* (juniper) is an invasive evergreen tree. We are evaluating the hypothesis that combinations of rainfall redistribution and warming that exceed the limits of plant acclimation will have the largest effects on growth, function, and competitive ability of these species. The research infrastructure is comprised of eight permanent rainfall exclusion shelters (9 x 18m). Simulated precipitation regimes include two patterns that vary seasonally in event size, but not in total annual rainfall or distribution of events. Rainfall redistribution withholds 40% of the summer rainfall (May – September) and redistributes it over the two preceding spring and two subsequent autumn months. Three monocultures and two grass-tree combinations were planted in each shelter in plots warmed with infrared lamps and paired controls. This design enables us to evaluate plant responses to altered rainfall patterns and warming both independently and in combination.

Rainfall redistribution significantly decreased soil water content by 31 % during the dry summer phase, but increased it only by 3 % in the spring and autumn wet phases as soils became saturated. Warming increased soil temperature (3 cm depth) by 0.5 °C and consistently reduced soil water content by approximately 1%. Warming had little effect on plant growth or grass-tree interactions, although there was an overall positive effect of warming on juniper growth. Rainfall redistribution increased grass growth in the first, but not in the second year of the investigation, and it reduced the proportion of reproductive tillers in both years. Both tree species showed a small negative growth response to rainfall redistribution. Intensified summer drought reduced rates of net photosynthesis (A_{area}) for oaks, but it did not affect A_{area} in the grass or juniper compared to the ambient rainfall pattern. The C₄ grass expressed less water stress and greater drought recovery of A_{max} than did either tree species in response to intermittent rainfall events during the intensified summer drought.

The presence of grass increased water stress in both tree species; however, the presence of juniper reduced water stress in the grass compared to monocultures. Shifts between competition and facilitation in grass-tree interactions resulted from seasonal changes in soil water content and species differences in phenotypic plasticity of root growth. Rainfall redistribution intensified grass-tree competition in the summer dry phase and reduced grass-tree facilitation in the wet autumn phase. These data document the occurrence of strong interactions among global change drivers, plant growth forms, and competition-facilitation dynamics that will mediate savanna responses to climate warming and rainfall redistribution.

Long-term manipulation of water and nutrients in Norway spruce stands

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The upper limit for forest biomass production on a particular site is set by the amount of incoming radiation. Actual production is, however, determined by the amount of radiation that is intercepted by the canopy during the active period of growth and, to a lesser degree, by the efficiency of conversion of intercepted radiation into biomass. If the natural fertility of a site is too low to maintain maximum leaf area index (LAI), hence "maximum" production, yield can in most cases be increased by supplying the limiting nutrients. Inadequate nutrition is a major reason for the difference between potential and actual yield, but in some regions potential yield cannot be achieved without improving the soil water conditions.

Results from two yield-optimization experiments in young stands of Norway spruce, in northern (Flakaliden, 64°07' N) and south-eastern (Asa, 57°08' N) Sweden, are presented after 15 years' treatment. The principal aim of the experiments was to eliminate water and mineral nutrients as growth-limiting factors. On the basis of repeated foliar analysis and predicted growth response the proportions and amounts of nutrients applied were adjusted annually. Imbalances in the nutrient status of the trees, induced by fertilization as determined by the foliage analysis, were successfully corrected by adjustment of the amount and composition of the fertilizer mix.

At the northern site, Flakaliden, there was a spectacular response to fertilization, with more than a tripling of annual volume growth, but with no additional effect of irrigation, indicating that air temperature is not the major direct constraint on tree growth at these latitudes. Temperature may, however, be influencing tree growth indirectly through effects on time of soil thaw, decomposition of soil organic matter, and mineralization of soil organic matter. Thus year to year variability in temperature may be influencing stem wood growth indirectly through the availability of nutrients and length of growing season. Irrigation alone or in combination with fertilization had no effect on production.

At the southern site, Asa, there was a doubling of yield, when fertilization was combined with irrigation. Fertilization without irrigation also resulted in a substantial yield increase, but was on average, 18% lower than in the combined treatment. During the same period irrigation alone increased yield by 12% as compared with non-treated control plots.

The growth responses were directly related to the development of LAI, and the amount radiation intercepted during the growing season. With fertilization full canopy closure (LAI > 8) was obtained at both sites, but the canopy development was slower at the low fertility site in the north than at the fertile southern site. In the south, however, full canopy closure was only obtained when fertilization was combined with irrigation.

The examples presented emphasize that most forest stands are growing at rates far below the potential level. By means of combined fertilization and irrigation, the yield of stemwood surpassed the best yields obtained by conventional silvicultural means.