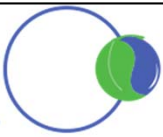


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Ecosystems and Environmental Change, Part 1



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University of California, Berkeley

4/23/2014

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The world about us is changing, in terms of temperature, CO₂, land use, N deposition, species loss, changing rain and weather patterns, extreme events, etc. This lecture and the next deal with how ecosystems are coping with a changing world.

Outline

- Background
- Methods
- Warming
- CO₂
- Rainfall
- Other
 - Ozone
 - N Deposition
 - Solar Dimming
 - Evaporation

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We cover background to the problem, how change is studied at the ecosystem scale and look at results

Anthropocene Era

(coined by Paul Crutzen, Nobel Laureate)



- Tenfold change in Human Growth, to over 7 billion, over the industrial period
- Human activity will release, in a few generations, the fossil fuels that have been sequestered over +100 millions of years
 - Concentrations of trace gases (CO_2 , CH_4) are exceeding historic values over the past 1 million years
- > 50% of land surface and use has been modified by mankind.
- More N is fixed Synthetically than Naturally
- > 50% of accessible fresh water is being depleted
- ~ 20% Marine fisheries are over exploited
- Extinction rates of species have accelerated
 - We're experiencing the 6th Great Extinction Period over Earth's History, the 1st caused internally.
- Land Use Change and Extinction Opens Niches for Invasive Species

http://www.igbp.kva.se/uploads/ESO_IGBP4.pdf

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For context, we are entering a new geological era, the Anthropocene. What is this and what does it mean to ecosystems?

Attributes of Global Environmental Change

- It is More than just Climate Change
 - Land use change, elevated CO₂, N Deposition, Species extinctions, etc
- Change is Fast
- Change is Multi-Factorial (CO₂, N, ppt, T, O₃, age, invasive species, disturbance)
- Change is Non-Linear, Hysteretic
- Change is Conditional on Antecedent Conditions
 - Down-regulation

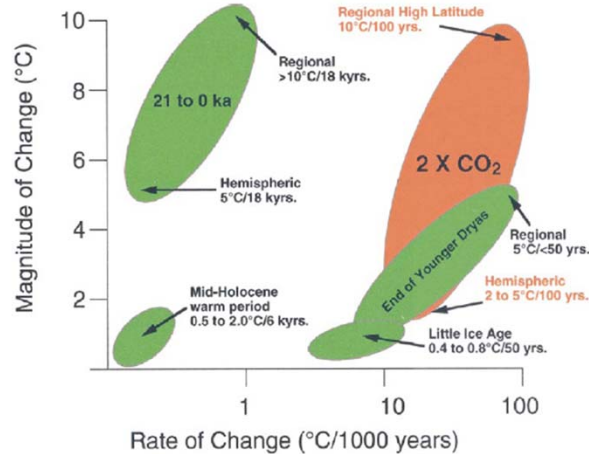
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Many of the lessons and lectures so far are poising us to deal with a new world, how to study it and how to interpret it.

Change that is Occurring is Fast and Large

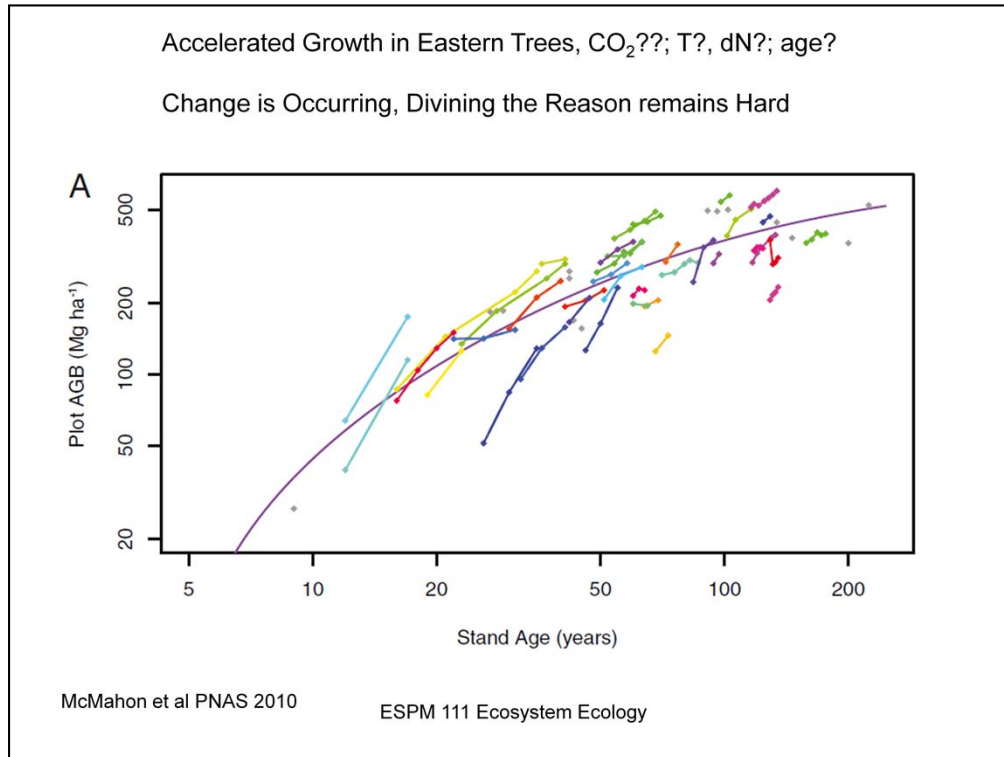
214

STEPHEN T. JACKSON AND JONATHAN T. OVERPECK



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This graph reinforces the point that current changes in temperature and CO₂ are different from what ecosystems experienced in the past in terms of rate and magnitude. During the last ice age the change in temperature was Large, but the change occurred slowly. And there was ecological shake out, vast northward movement of forests, loss of megafauna (wooly mammoth, saber tooth tiger, etc)



This paper is showing that above ground biomass of forests in the east are increasing. But why? Is it age, a CO_2 , temperature or N deposition effect? How do we separate these causes and effects from data? We do have to separate ecological age effects from observed trends when attributing other factors. Residual analysis is important. So here we see the theoretical line of changing above ground biomass with age and super imposed are vectors measuring change at give plots along this chrono sequence. Many of the vectors have slopes steeper than the age effect.

Difficulty of Extracting Cause/Effect Information from Time Series

Table 1. Hypotheses to explain accelerated recent growth of forest stands

Hypothesis	Description
Increased temperature	Higher temperatures over the growing season (or growing degree day sums) can increase metabolic rates and therefore, lead to more rapid carbon sequestration.
Increased growing season	Longer growing seasons (especially earlier springs) has been observed in many systems. A longer growing season would allow stands earlier leaf-flush and therefore, increased carbon sequestration.
Increased CO ₂	Higher atmospheric CO ₂ can increase photosynthesis and lead to higher biomass accumulation.
Nutrient fertilization	Nitrogen and phosphorus fertilization from agricultural and urban runoff can increase tree growth. Atmospheric deposition of nitrogen has increased in urban and industrial regions in the United States in recent decades and could lead to soil fertilization as well.
Community composition	Some pioneer species tend to grow faster than others, especially sweet gum (<i>Liriodendron styraciflua</i>) and tulip poplar (<i>Liquidambar tulipifera</i>). An influx of these species into a plot or a preponderance of fast-growing species recently becoming dominant could lead to an increase in biomass accumulation.
Demographic stochasticity	Although a stand may follow the ensemble biomass-accumulation pattern, random deaths of large trees can lower the stand biomass, and rapid regeneration will quickly increase the biomass as if the plot were, through a death, moved to a younger state.

McMahon et al 2010 PNAS

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The authors do not conclude which factors are causing the change, but lean towards the combination of temperature, CO₂ and longer growing seasons. Water deficits are not an issue in the east, so warmer temperature can be viewed as a positive factor

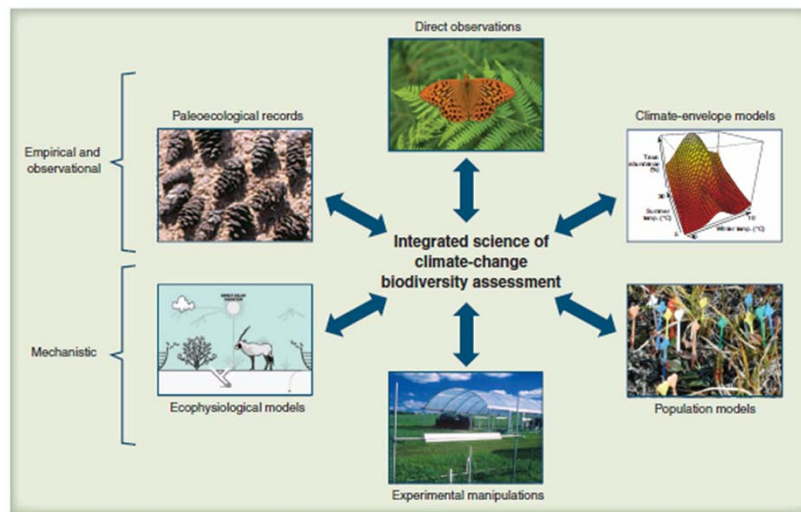
Responses to Environmental Change:
Ecological Lessons your Mom, or Snarky Brother, may
have taught you

- Tolerance
 - ‘Put up or shut up’
- Avoidance
 - ‘Get out of the sun or you’ll get a sun burn’; ‘If its too hot in the Kitchen, get out’
- Acclimation
 - ‘When the going gets tough, the tough get going’
- Adaptation
 - ‘put on your sunscreen, so you won’t get skin cancer’
- Dispersion/Movement/Migration
 - ‘Get the hell out of Dodge’
- Extinction
 - ‘Congratulations, you’ve won the Darwin Award’

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Plants don’t move fast or far in short terms, hence they have to deal with what they got. What are the options.

Ways to Study Ecological Change



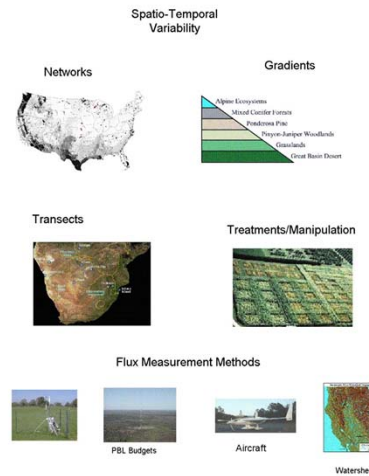
Dawson et al 2011 Science

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Observations, models, manipulative studies are among the arrows in our quiver to study ecological change. We can look at past records via pollen and spores in lake sediments, tree rings and stable isotope records. Gradient studies provide a natural laboratory.

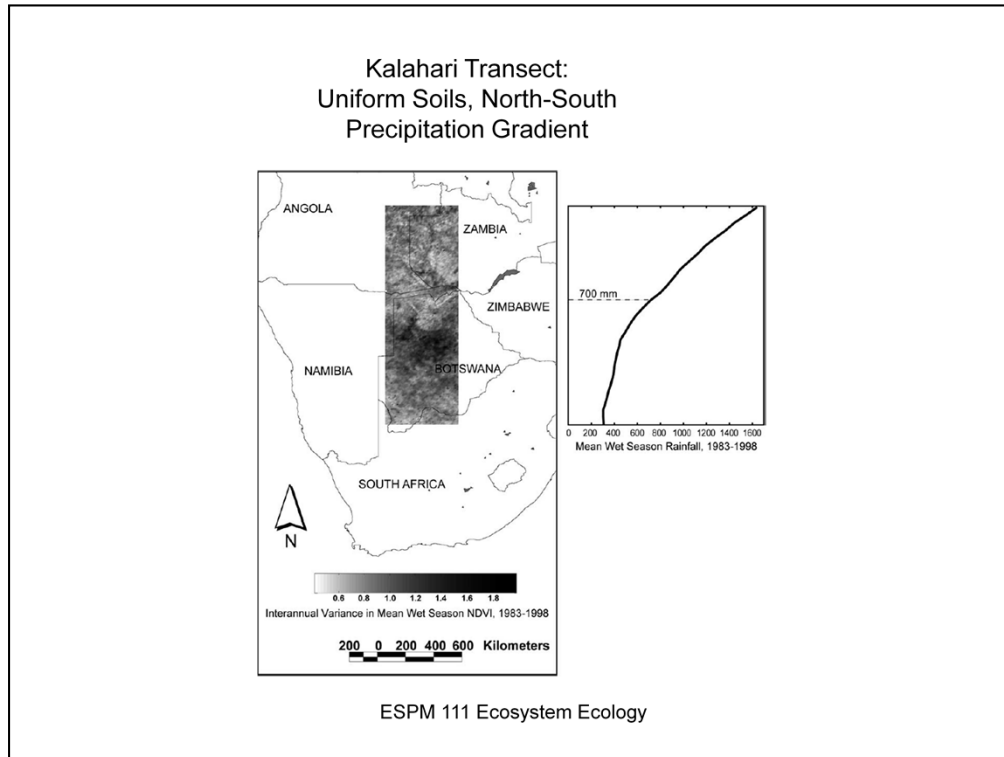
Experimental Manipulation & Methods

- Long-Term Monitoring Networks and Natural Experiments
- Transects/Gradients
- Open-Top Chambers
- Free-Air Exposure (FACE)
- Heating
- Exclusion/Addition
 - Rain, fertilizer

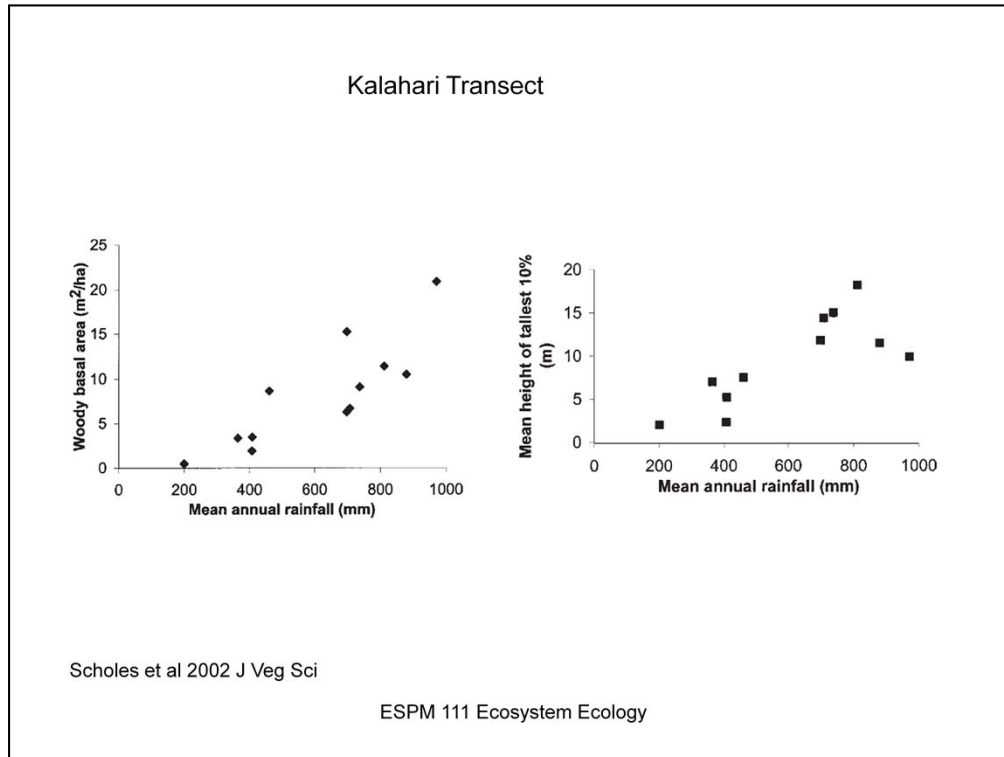


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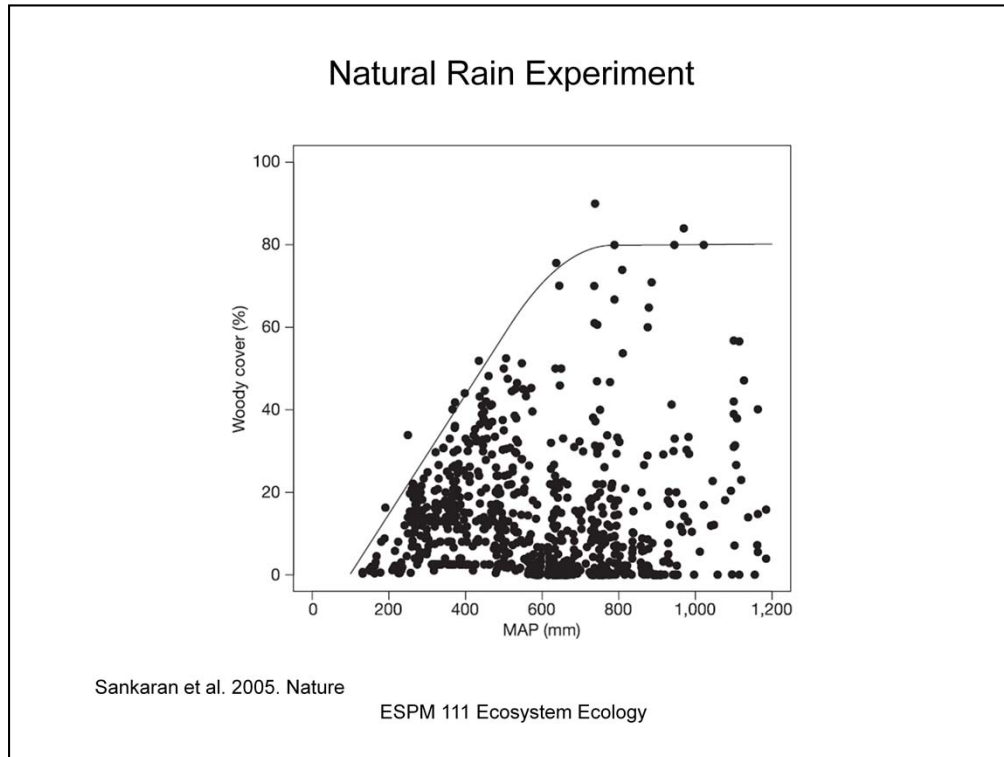
List of methods used. We will go into greater detail.



Natural gradients are great, if one can avoid artifacts by different soils, for example. The Kalahari transect is unique due to its uniform sands and strong precipitation gradient. One can study the 'equilibrium' response, operating on short to long time scales, of ecosystem-atmosphere interactions to rain, in terms of the physiological response, the type of plants and the leaf area index that is established.



Woody basal area and tree height are positively correlated with annual rain fall



Rain yields a boundary line analysis on percent of woody cover. Of course other limiting factors cause a deviation from the upper boundary line.

Open Top Chamber



Elevated CO₂ and O₃, warming

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One can enclose plants and alter their conditions. This approach is more artificial, has artifacts (due to the age and stature of the plant and the conditions of the chamber, and can be only short term, due to funding and interest

Eco-cosms



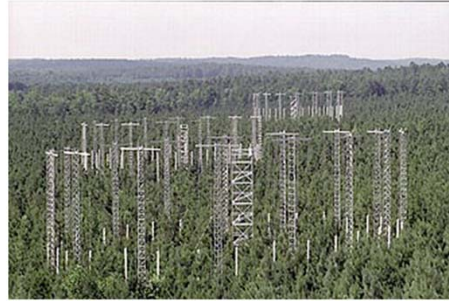
Biosphere II



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Small ecosystems have been established at various institutes. On one hand, one can control the environment in a prescribed manner, and possibly well. But what is an ecosystem? What needs to be in it in terms of plants, species, soils and the modulation of conditions.

Free-Air Carbon Exposure (FACE)

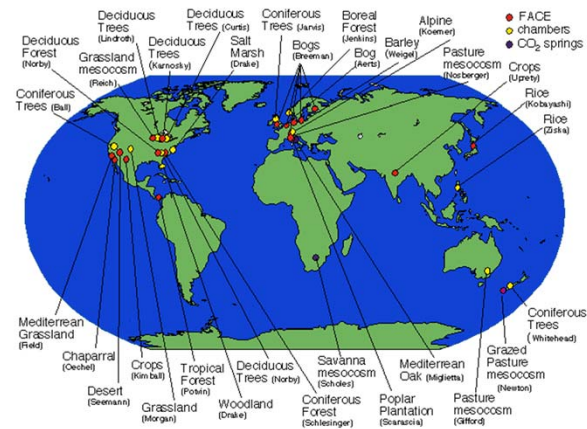


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Free air exposure systems attempt to let plants grow under natural conditions and just goose the CO₂ by venting it upwind. The approach is very expensive as most CO₂ diffuses away, and large sources are needed to maintain elevated levels near the plant.

Questions arise to which CO₂ concentrations to choose? What about replications? How big should the plots be? Can they be sub sampled regularly?

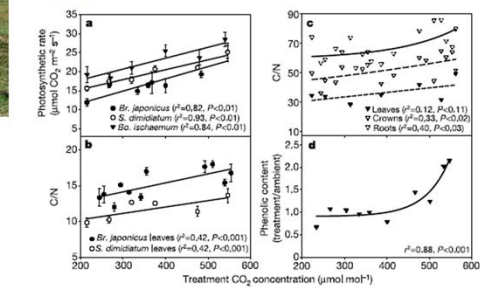
Elevated CO₂ Studies



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FACE is popular, used world wide over crops, forests, plantations, wetlands, grasslands, deserts, etc, etc

CO₂ Tunnel, Temple, TX and Duke



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Gill et al Nature, 2002

Clever method to impose a natural CO₂ gradient as air moves through the tunnel with a continual carbon sink.

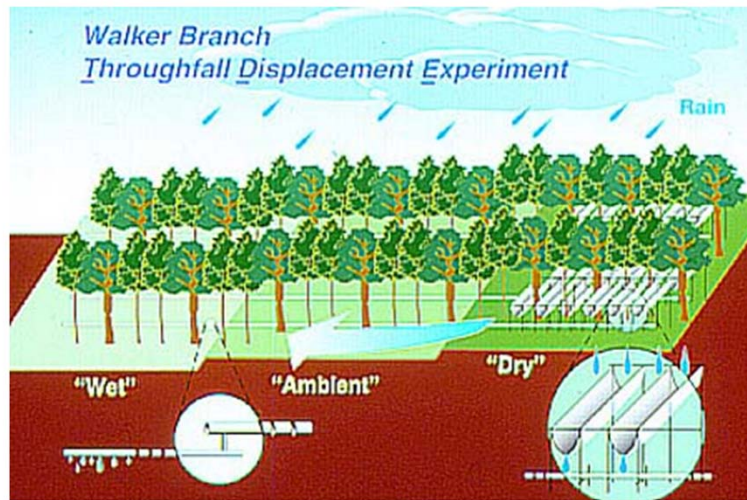
CO₂ Exposure Methods: Pros and Cons

- Pots
 - Seedlings or saplings, not representative of mature trees
 - Plants become root-bound
 - No Ecosystem interactions or competition
- Chambers and Soil monoliths
 - Artificial light, humidity and temperature levels in the chambers
 - No ecosystem processes
 - Limited to low stature plants
- Free-Air Carbon Exposure Studies (FACE)
 - Field conditions
 - Plants compete for light, water and soil resources
 - Expensive, much CO₂ is Advected Away.
 - Control at set point varies by +/- 10 to 20%
 - Expensive to Replicate
 - Can't sample vegetation of Treatments periodically without destroying treatment

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Explicit list of pros and cons. I don't advocate we should not attempt to use these methods, but be careful on how we interpret the data.

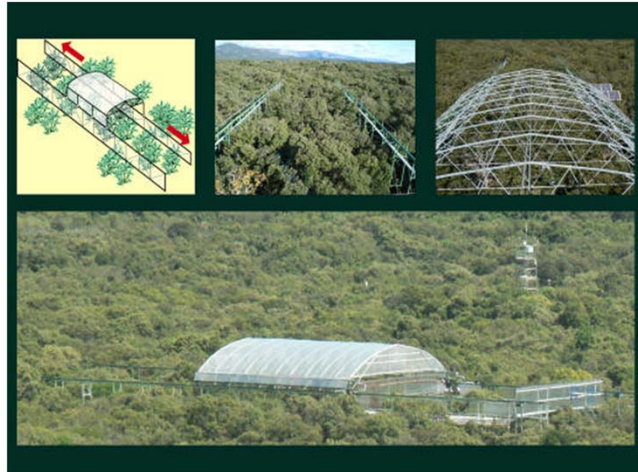
Rainfall Addition/Subtraction



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Rainfall can be added and subtracted. Large scale field manipulations studies suffer many of the slings and arrows launched at FACE studies.

Mobile Rain Shelter, Puechabon, FR



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Laurent Misson +

Colleagues in France developed a mobile rain shelter. Quite an engineering feat as this is the land of the Mistral, where 100 km/hr winds were common. Replication remains a concern.

Rain Exclusion, Amazon



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Another example of rain exclusion in the tropics

Rain Addition/Exclusion Pros/Cons

- Rainfall effects are non-linear
 - Need 3+ treatments to characterize Non-linearity and know where the breakpoints are.
- Method is expensive and difficult to replicate
- Timing of rainfall may be as important as amounts added/subtracted
- Need Long term studies to sort out the short (physiological) and long term (lai, species, rooting depth) effects

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Pros and cons

Ecosystem Warming Experiment, V1



Infrared Lamps Mimic CO₂ IR Forcing

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Warming experiments have received much discussion on whether to expose plants to an elevated temperature or an elevated infrared flux density that mimics CO₂ greenhouse effect. John Harte has favored the elevated IR effect, in the Colorado Mountains and this has been copied by many.

Warming Has different effects during summer and Winter



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Rocky Mountain Biological Lab, photo of Saleska. Warming in the mountains affects not only plants during the growing season but snow, snow cover and its water input

Ecosystem Warming Experiment, V1a



Yiqi Luo, Univ OK

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Visual difference of plants under the heating lamps, during the wetter period.

Passive Nighttime Warming System



Josep Peñuelas, Barcelona

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A cost effective and less energy intensive way to warm ecosystems is with a passive shield at night, reducing long wave energy loss to the sky

Tree Warming Expt, v2



Air Conditioning Warms Air Temperature

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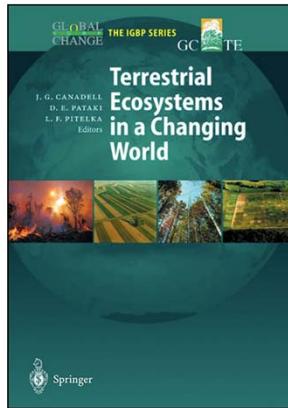
The more elaborate is to just air condition the system

Warming Experiment: Pros and Cons

- Alter Radiation
 - Infrared lamps mimic predicted change in CO₂ forcing
 - Lets plants adjust surface energy balance (eg albedo, surface resistance, leaf temperature)
- Alter Temperature
 - Imposes a prescribed temperature differential
 - Air temperature is not the same as surface temperature
- Big Electricity Bills \$\$\$ Warming the system
- Winter Effects differ from Summer Effects
- Co-Variation with Temperature and Water Balance

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Results from Global Change Experiments

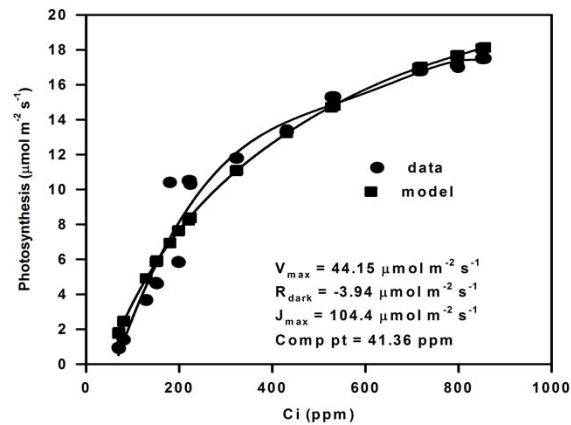


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Two excellent resources on global change ecology

Photosynthesis vs CO₂

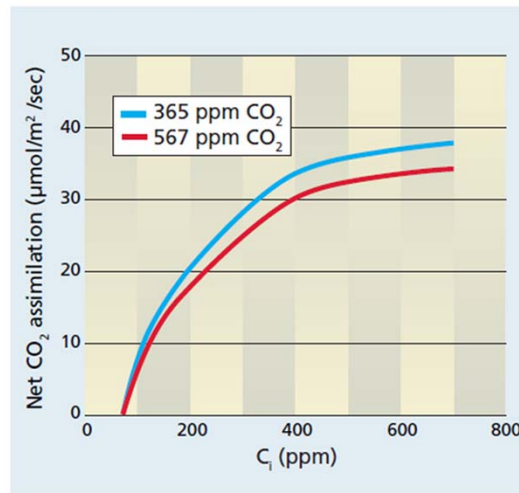
D 205; Oak leaf, canopy
Tleaf: 25C; vpd: constant flow 100
Qp: 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$



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Physiologically CO₂ can be viewed as good for plants. More CO₂ more photosynthesis. The questions arise on how to sustain this and is it sustainable for natural ecosystems where light, water and nutrients may become limiting as plants grow bigger and bigger.

Down-Regulation of Photosynthesis based on CO₂ Growth Environment

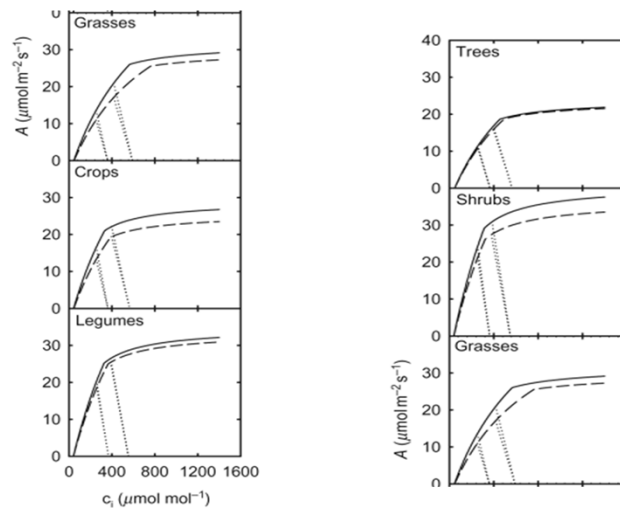


Ainsworth and Rogers 2007, PCE; adapted from Bloom, 2009 Cal Ag

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One of the more important scale emergent facts is a down regulation in the response of photosynthesis with CO₂, with growth environment. Plants grown under higher CO₂ levels reach a lower maximum photosynthetic rate at high CO₂.

Down-Regulation of A-Ci Occurs across many Plant Groups



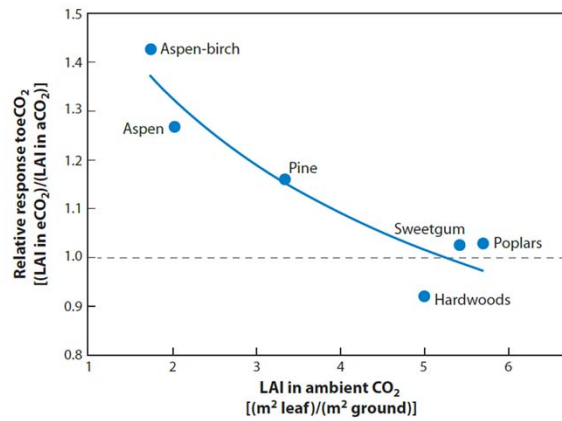
Ainsworth and Rogers, 2007, PCE

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This effect is wide spread.

Check table 1 for V_{cmax} and compute A-Ci curves and redraw, dashed elevated $\text{CO}_2 \sim 560$ ppm, solid ambient $\text{CO}_2 \sim 365$ ppm

LAI Increases with Elevated CO₂ only if the Canopy is Not Closed

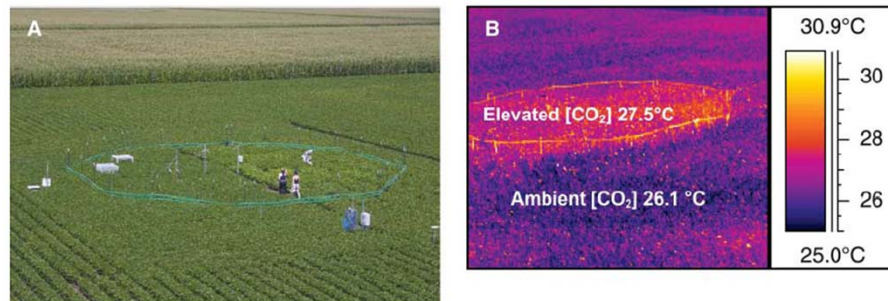


Norby and Zak, 2011 Annual Reviews Ecology Systematics

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Good example of the role of light limitation on not fostering additional increments of leaf area once the canopy closes with an LAI of about 6, which intercepts over 95% of incident sunlight

**CO₂ and Crop Temperature:
Induced Stomatal Closure Increases Surface Temperature**



Long et al., 2006 Science
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High CO₂ causes stomatal closure, which will reduce transpirational cooling and warm the leaves of the plants more. Here is data from the soybean studies of Steve Long in Illinois. IR camera shows the warmer soybeans.

Elevated CO₂

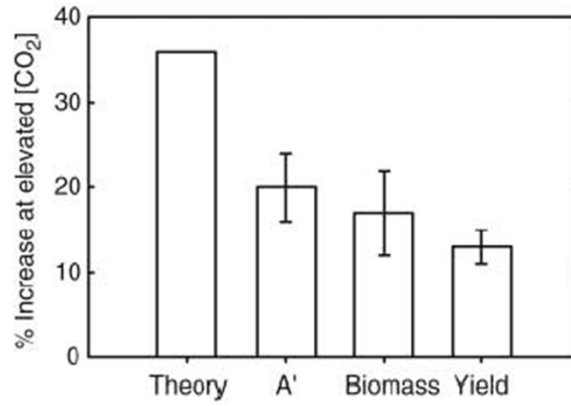
- *'... the rate of CO₂ uptake per unit leaf area is a rather unreliable predictor of plant growth and the cascade of follow –up ecosystem processes'*
 - Korner et al 2007 GTCE



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Effect of Elevated CO₂ Diminishes as One Follows the Carbon Cycle Cascade:

A_{theory} > A_{measured} > Biomass > Yield



Long et al 2006 Science

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Relation between elevated CO₂ on theoretical and measured increase in photosynthesis and how this carbon is used to produce biomass and yield. Each step has a smaller incremental increase, though all are positive and greater than 10%

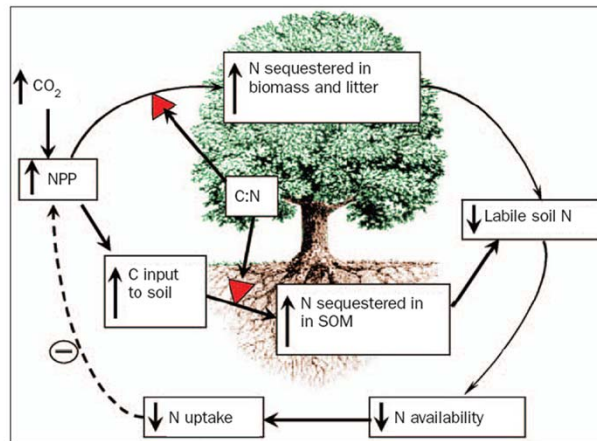
Elevated CO₂: Direct and Indirect Effects

- **Fast-scale, Physiological**
 - Photosynthesis, ++
 - Stomatal conductance, -
 - Transpiration, +/-
- **Slower scale, Ecological/Biogeochemical**
 - Growth, +
 - Bigger plants grow faster, 'compound interest effect'
 - Below ground allocation and Resource Acquisition, +
 - Mineralization, -
 - Down-regulation in Photosynthesis
 - Respiration, +
 - Water Balance
 - Water Use Efficiency increases with stomatal closure
- **Slowest scale, Community Dynamics**
 - Species change and competition
 - Vulnerability to Disturbance

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We have to think about fast and slow responses, what they affect and how they interact and sum to affect the net ecosystem response

C-N Interactions and Feedbacks



Luo et al. 2004 Bioscience

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This feedback chart shows some of the processes that are amplified or reduced with a perturbation of CO₂. More CO₂ increases photosynthesis, leads to more growth and N sequestration. If C:N increases, N is diluted in the litter quality, which can reduce the amount of labile N for the next go round of the cycle, leading to a down regulation of photosynthesis.

Elevated CO₂, Facts and Myths

- Enhances Photosynthesis
 - Down-Regulation in Ps from Nutrient Limitations
- Reduces Stomatal Closure
 - Direct Effect
 - Reduces Transpiration and Increases WUE
 - In Direct Effect and Positive Feedback
 - Elevated Leaf Temperature, augments Transpiration
- Greater Growth and Leaf Area
 - Bigger plants grow faster. +; effect saturates at high LAI
 - Bigger plants transpire more
 - Soil moisture pool depleted faster: -
- Herbivore Interactions
 - Insects eat more foliage to compensate for lower N quality of leaves

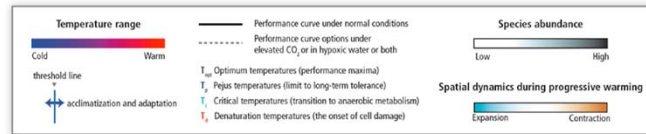
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Effects of Temperature are + and -

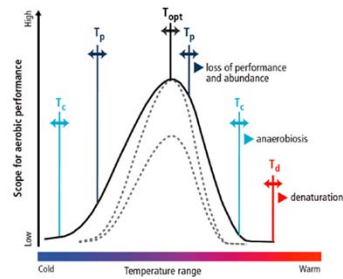
FINAL DRAFT

IPCC WGII AR5 Technical Summary

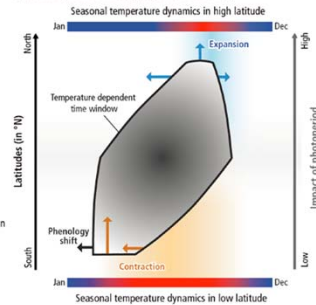
Do Not Cite, Quote, or Distribute Prior to Public Release on 31 March 2014



A) Thermal windows for animals: limits and acclimatization



B) Spatial dynamics during progressive warming

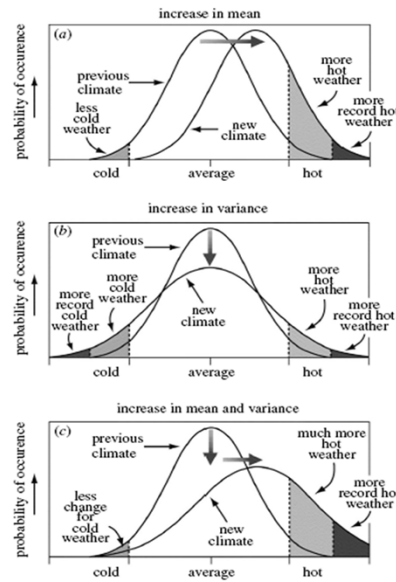


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The effects of temperature are conditional, as the biological response is highly non linear

IPCC AR5 working group 2 report

Mean Temperature is not the only relevant biological temperature

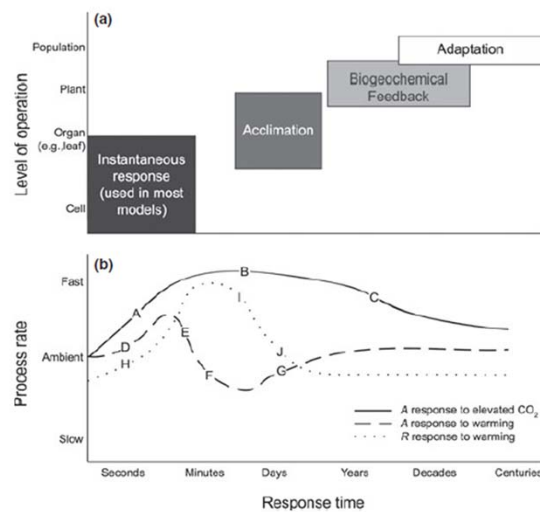


Porter and Semenov

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The effect of temperature is complicated, as there are many temperatures of biological interest, average, minimum, maximum, range, extremes

Role of Temperature Acclimation and Adaptation

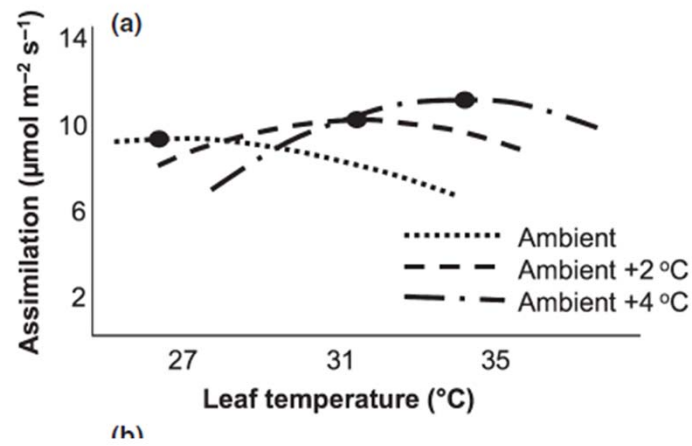


Smith and Dukes 2012 GCB

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Temperature effects and responses occur on short and long time scales, including direct physiological responses, acclimation, feedbacks and adaptation

Temperature Acclimation with Growing conditions

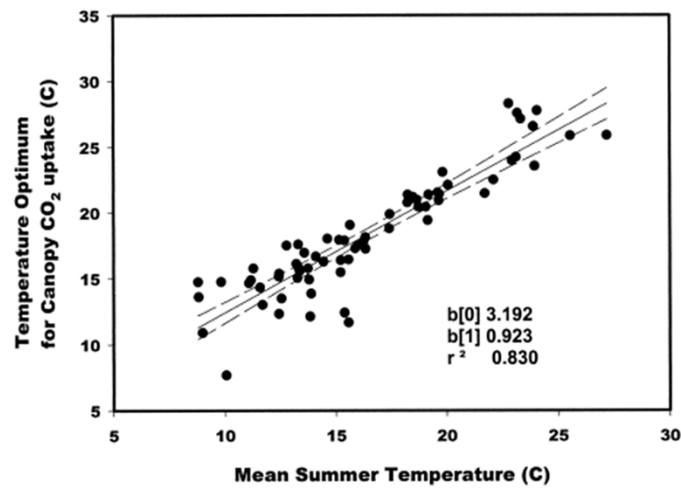


Gunderson et al. 2010 Global Change Biology

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The physiological temperature response to photosynthesis is non linear with a broad optimum, but the optimum acclimates and shifts with growing temperature. Yet, another scale emergent property

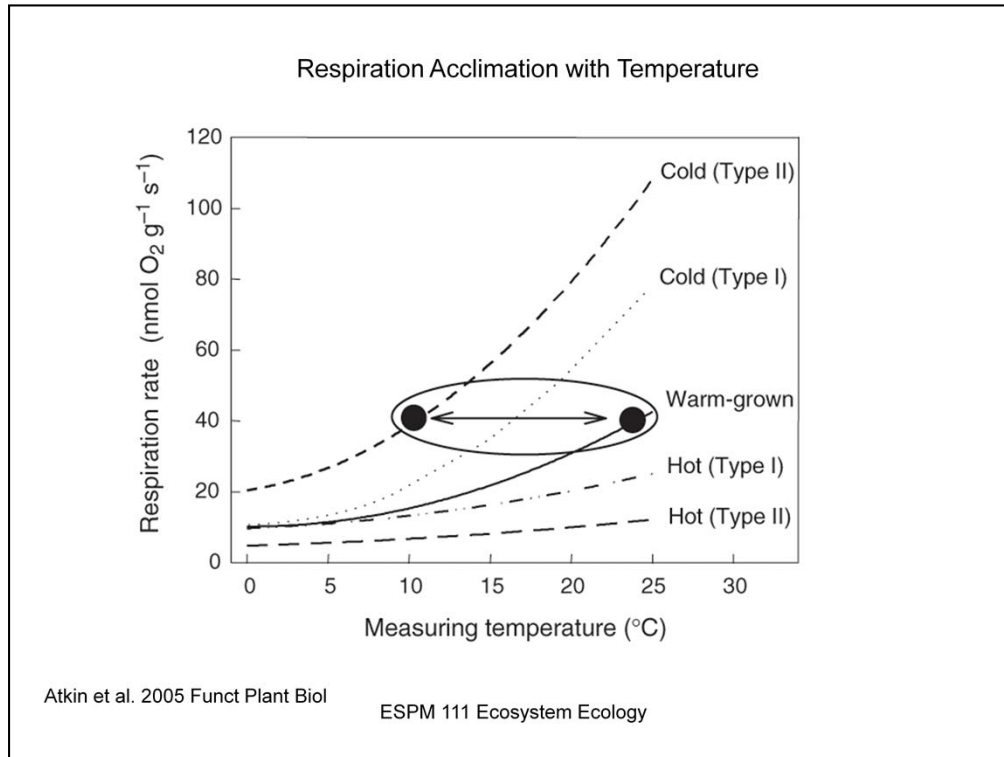
Optimum Temperature for Canopy Photosynthesis Acclimates
with Summer Growing Season Temperature



Baldocchi et al. 2001 BAMS

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Data from the fluxnet project indicating that ecosystem response of carbon assimilation to temperature acclimates with growing season temperature.

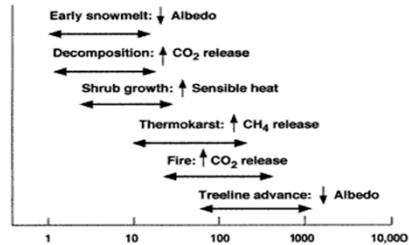


Respiration-temperature response, too is a function of growth conditions.
Atkin et al 2005 Functional Plant Biol

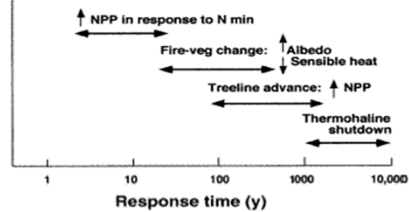
Direct and Indirect Effects of Temperature

220 F. S. CHAPIN III *et al.*

Positive feedbacks to warming



Negative feedbacks to warming



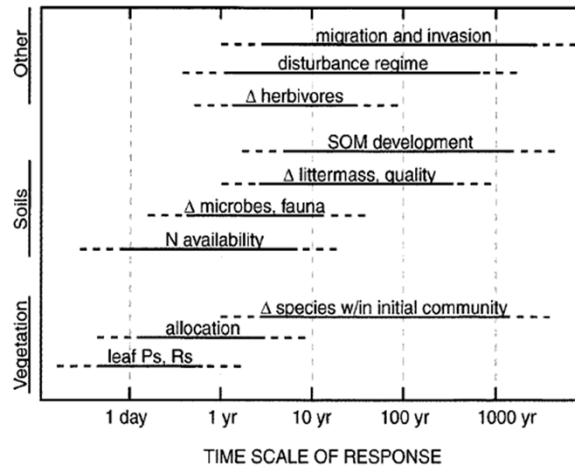
Missing are Insect and pest infestations; drought, accelerated mortality

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Examples of biogeochemical feedbacks, fire, growth, species migration, etc With temperature and ecosystems there are many direct and Indirect effects to consider that have negative and positive feedbacks. What is missing on this figure?

Try insect infestations, drought

Warming and Ecosystems

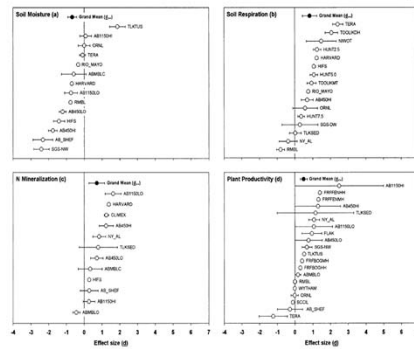


Shaver et al 2000 Bioscience

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Meta Analysis of Warming Studies

- Soil Respiration increased by 20% with 0.3 to 6 C warming
- Net N mineralization increased by 46%
- Plant Productivity increased by 19%



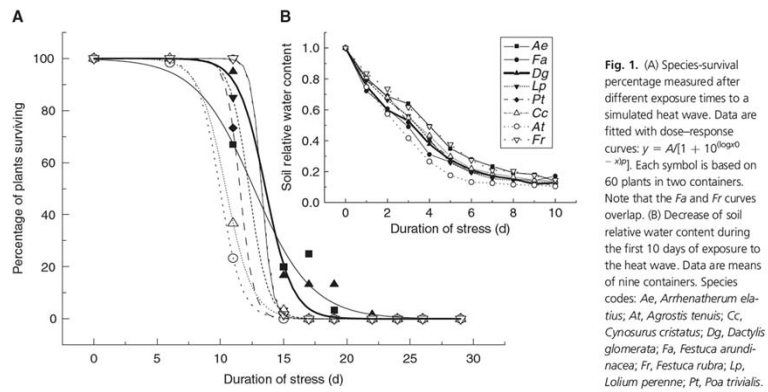
$$d = \frac{\overline{X_{\text{exp}}} - \overline{X_{\text{control}}}}{\text{std dev}}$$

Rustad et al. 2001 Oecologia

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Soil warming experiments have been conducted and analyzed with meta analysis.

Duration of Heat Stress and Mortality



Milbau et al 2005 *Physiologia Plantarum*

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Duration of heat stress is important, too

Long Term Warming Experiment

- Harte investigated carbon-cycle responses to climate changes by combining results from a controlled 15-year ecosystem warming experiment in montane grassland with observational data from before and during the recent drought.
- They found that both experimental warming and real-world drought induced substantial soil carbon loss in the study system, and that the same mechanism, a drying-induced shift in plant species composition and an associated decline in community productivity, provides a common explanation for these declines in soil carbon. warming expt

Harte et al 2006 ERL

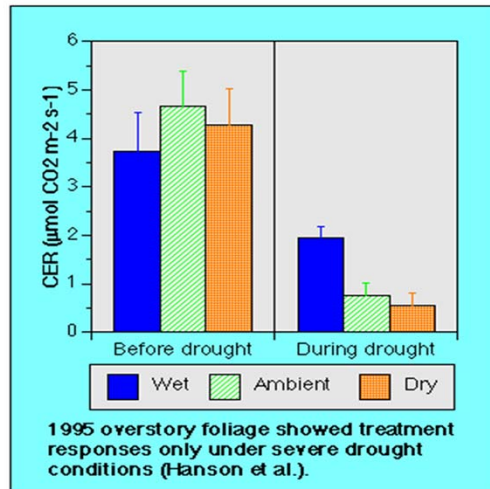
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Rainfall Exclusion or Addition

- Studies and Results are Conditional
 - Treatment addition/removal
 - Climate Zone
 - Research Results seem Difficult to Publish

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In Temperate Zones, Wet years are WET, so reduction in ppt has little effect

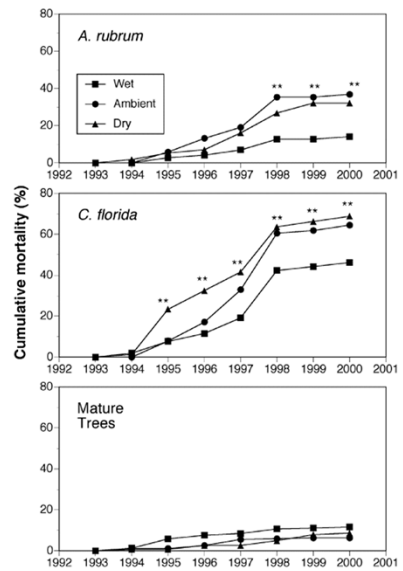


In Temperate Zones, Dry years are DRY so a reduction is observed in all Treatments

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Rain manipulation studies in eastern deciduous forests have been difficult to maintain treatments; an example why I like natural experiments, natural gradients and work in California with our predictable and repeatable drought.

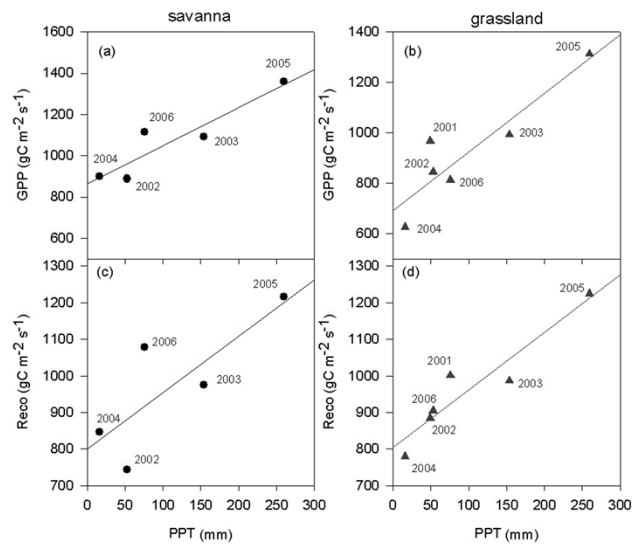
Mortality is Increased with Long-Term Rain Treatments



Hanson et al. ORNL

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Carbon Fluxes of CA (Mediterranean) ecosystems respond best to rain during the Growing Season

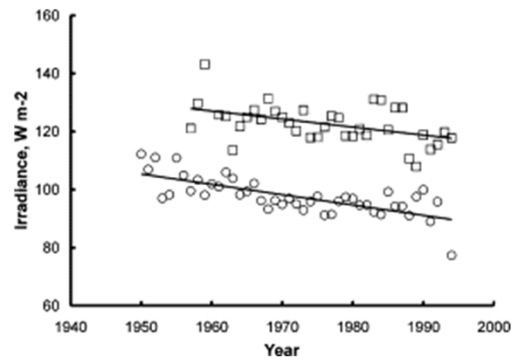


Ma et al. 2007 AgForest Met
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Here are data from our field sites in the Sierra foothills. We find that rain during the spring growing season best describes year to year changes in GPP and Reco

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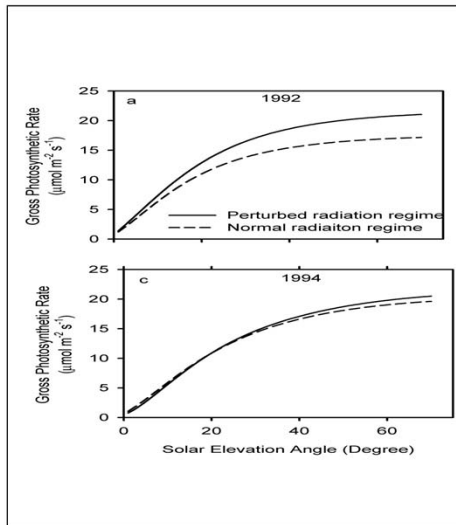
Pollution and Dimming of Solar Radiation



Stanhill and Cohen, 2001

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Impact of Dust on GPP



Gu et al., Science, 2003

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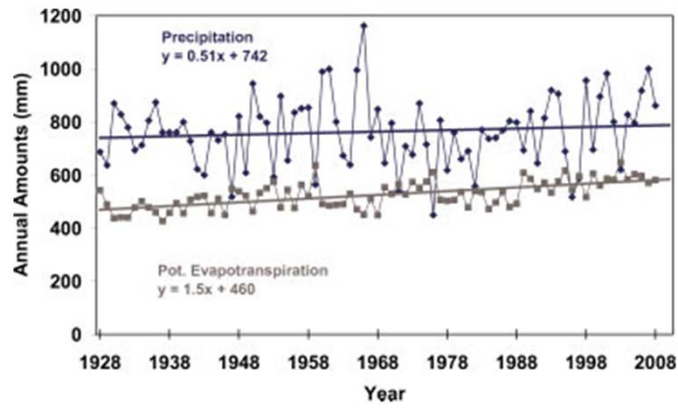
Evaporation and Climate Change

- In Principle, Global Warming Should
 - Accelerate and Water Cycle
 - Increase Evaporation
 - Increase Cloud Cover
 - Increase Precipitation
 - Reduce Solar Radiation
 - Negative feedback on Evaporation

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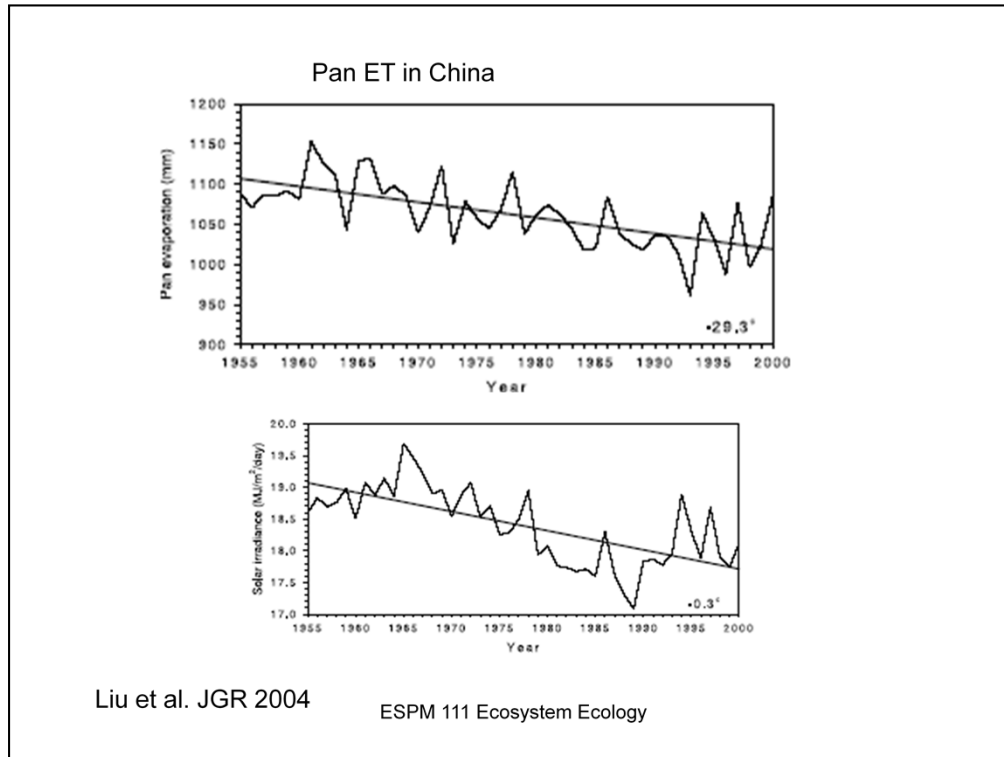
80 year Trend in Evaporation

Wageningen, Netherlands



Jacobs et al 2009 Int J Climatology

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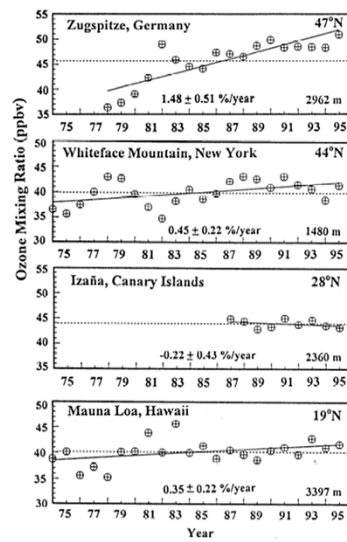
Pan evaporation may be decreasing. One would think that the hydrological cycle is accelerating and evaporation is increasing. But there is the pan paradox and actual and pan evaporation are complimentary.

Explanations

- Pan Evaporation paradox (Brusaert and Parlange, 1998)
 - Actual and pan evaporation exhibit complimentary behavior.
 - observation of decreased pan evaporation indicates that actual evaporation is increasing in semi-arid regions,
- global reduction in pan ET reflects the dimming of radiation due to aerosols
 - Roderick and Farquhar
 - Liu et al. JGR

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Tropospheric Ozone Trends



Oltmans et al 1998 GRL

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Ozone-CO₂ Interactions

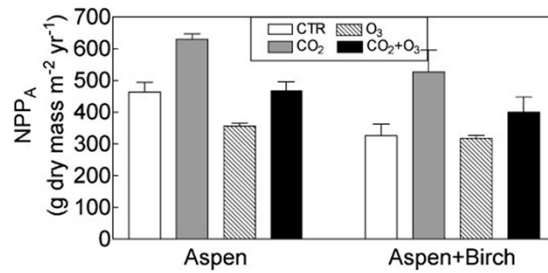


Figure 14 Comparison of NPP_A for mixed trembling aspen and birch trees grown in ambient or control atmospheric CO₂ concentration (CTR), enriched CO₂, elevated ozone, and ozone + enriched CO₂ FACE rings. (Data were generously provided by E. Kruger, University of Wisconsin.)

Gower, 2003, Ann Rev Environ Res

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Ozone, N and forests

- Decreased visibility by sulphate particles
- Increased tropospheric Ozone
- Depletion of Cations in soil and mobilization of aluminum
- Tree dieback (spruce and maple, NE)
 - disruption of Ca nutrition and Al toxicity
 - Cold tolerance disrupted

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Driscoll et al

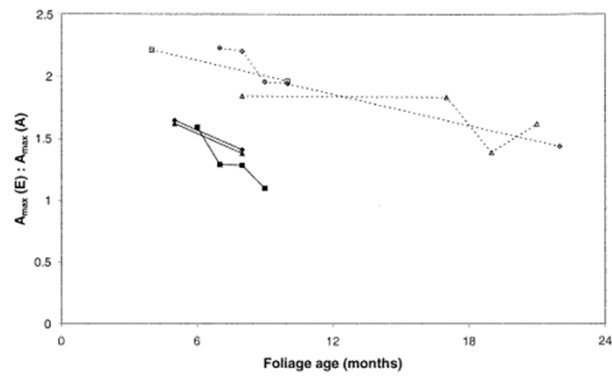
CO₂ Sink Saturation

CO2 fertilization on NPP	Sink
Nitrogen deposition fertilization on NPP	Sink
Air pollution effects on NPP	Reduced sink
T and ppt on NPP	Sink/reduced sink
T and ppt on Rhetero	source
Permafrost thawing	source
Shift in disturbance (fire, insects, disease)	Source/sink
Shift in vegetation	Sink/source
Afforestation/reforestation	sink
Forest regrowth, abandoned cropland	Sink/Reduced Sink with Age
Vegetation thickening and encroachment	Sink/Reduced Sink with Age
Soil erosion and burial	source./sink
Crop management	Source/sink
Deforestation	source
Peatland drainage	source

Canadell et al 2007 GTCE

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Down Regulation of Photosynthesis: European Forests

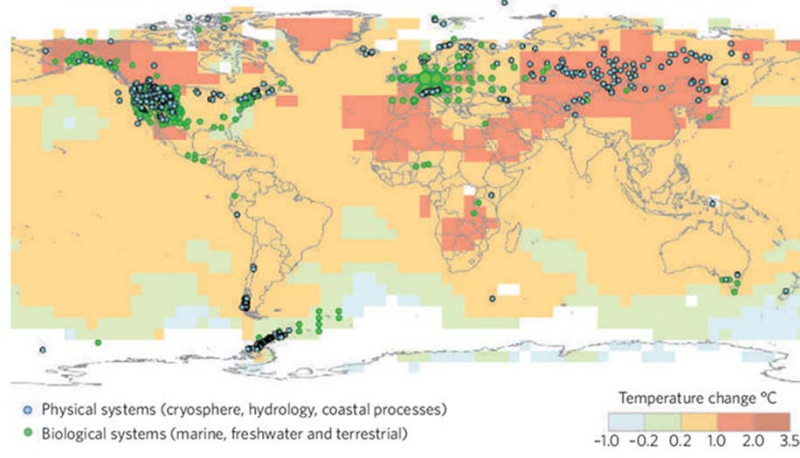


Medlyn et al. 1999

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Norby

Observed changes in physical systems, biological systems and temperature for 1970-2004



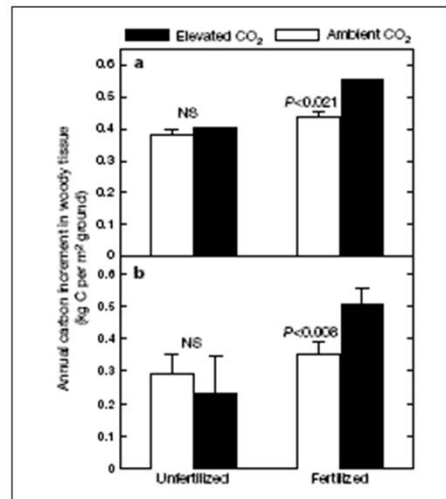
IPCC 2007

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Soil Fertility Limits C sequestration at Duke Forest



Oren et al. 2001 Nature



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CO₂ and N interactions

- Evidence from long-term field studies suggests that both progressive N limitation under eCO₂ and a significant interaction between CO₂ and plant available N supply that constrains NPP responses to eCO₂ are likely to be common, although not ubiquitous, in many natural and managed ecosystems.
- The combination of progressive N limitation and an interaction of CO₂ and plant available N supply will likely lead to smaller NPP enhancement under eCO₂ than widely anticipated.

Reich et al. 2006 Ann Rev Ecol

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Global Change and Ecosystem Issues

- Population Growth
 - Climate Change
 - Rising CO₂, Sea level rise, Global warming, changing ppt patterns (+/-)
 - Stratospheric ozone depletion
 - uv effects, cancer, mutations
 - Good News, it is being Mended
 - Land Use Change
 - Forest fires, biomass burning, conversion to agriculture
 - Water Quality and Fresh Water Depletion
 - Ground water depletion, lake/sea depletion (e.g. Aral Sea)
 - Air Pollution
 - Rising ozone and aerosols
 - Good News it is Improving
 - Soils Degradation, Subsidence and Erosion
 - Toxic chemicals and hazardous waste
 - Loss of Biodiversity
 - Nitrogen Loading on Ecosystems
 - Acid rain, eutrophication, hypoxia
 - Marine Resources
 - Over-Fishing
 - Good News it is being Mended
 - Ocean Acidification and Coral Bleaching
- ESPM 111 Ecosystem Ecology

RESPONSE OF MULTISPECIES SYSTEMS TO ELEVATED CO_2

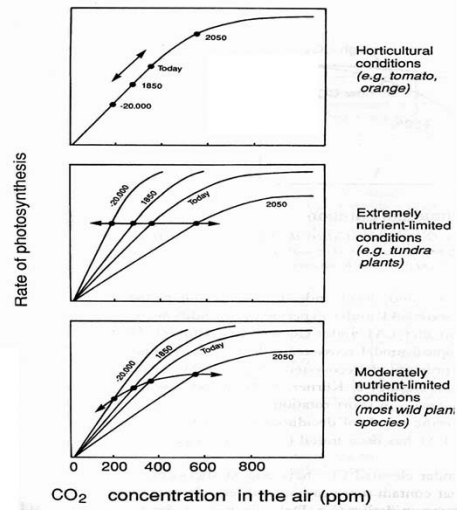
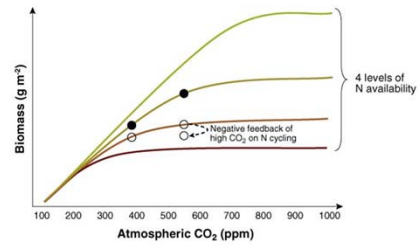
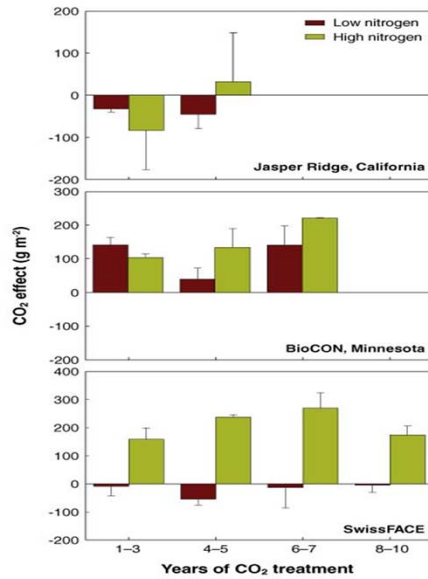


Figure 3.2 Photosynthetic adjustment to changing CO_2 concentration: a multitude of possible long-term responses.

CO_2 and Forest Photosynthesis



Effect of Duration of Study and N Load

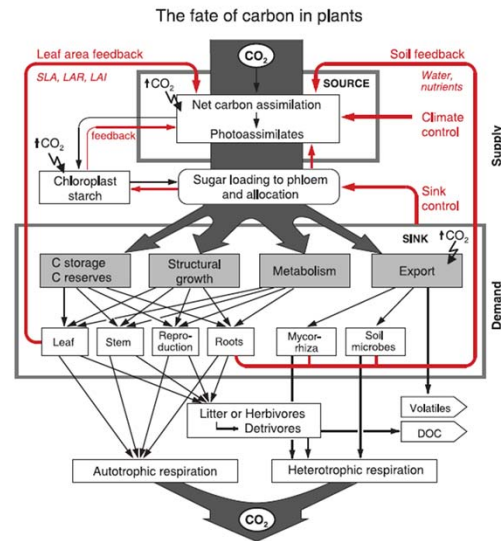


Reich PB, et al. 2006.
Annu. Rev. Ecol. Evol. Syst. 37:611–36

Reich PB, et al. 2006.
Annu. Rev. Ecol. Evol. Syst. 37:611–36

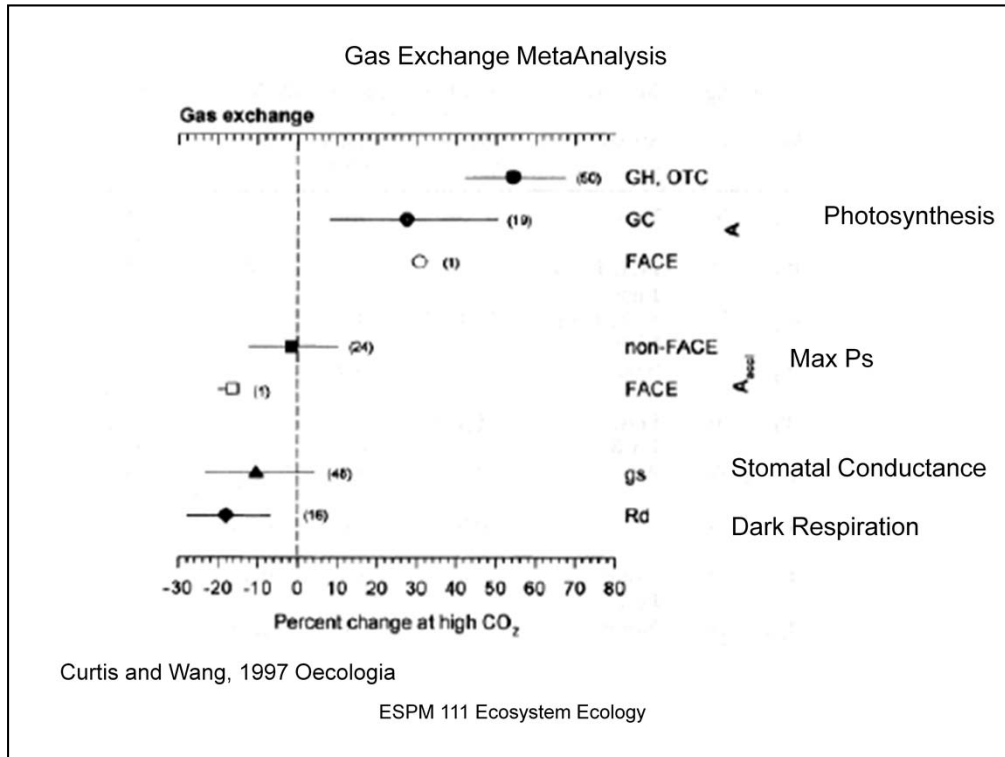
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But 'Everything is Connected', W. Silver



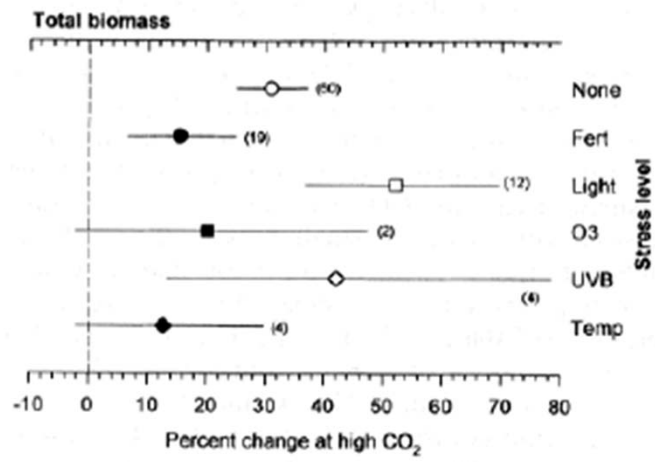
Körner, 2006 New Phytologist

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Curtis meta analysis

Biomass Meta Analysis

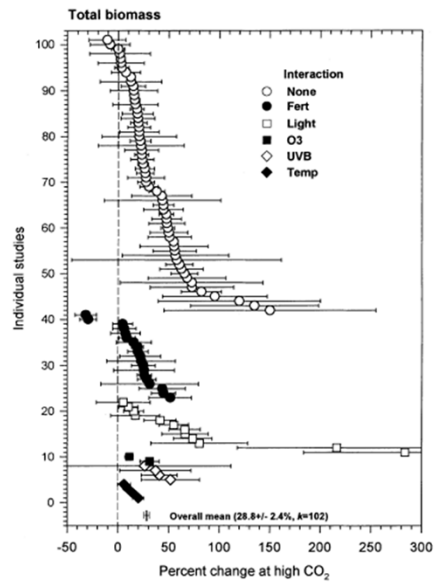


Curtis and Wang, 1997 Oecologia

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Curtis Meta analysis

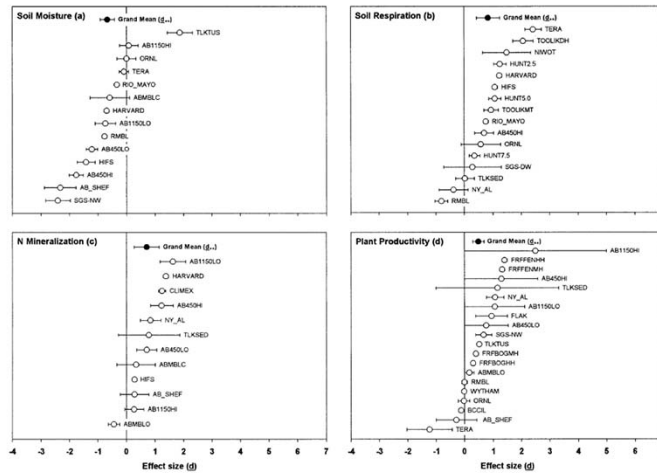
MetaData Analysis



Curtis and Wang, 1997 *Oecologia*

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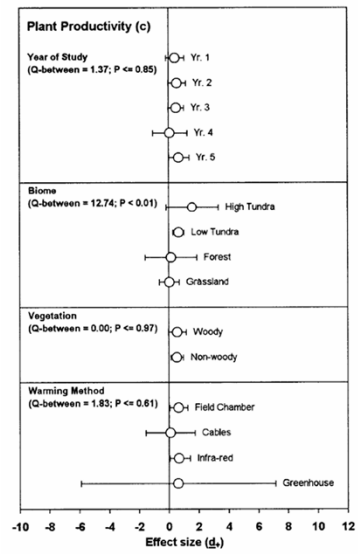
- Meta Analysis of Warming Studies



$$d = \frac{X_{\text{exp}} - X_{\text{control}}}{\text{std dev}}$$

Rustad et al 2001, Oecologia Warming Meta analysis

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Rustad et al 2001, Warming Meta analysis

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Meta Analysis

- Synthesis of
 - Treatments
 - Methods
 - Plant Functional Types
 - Physiological Processes
 - Duration

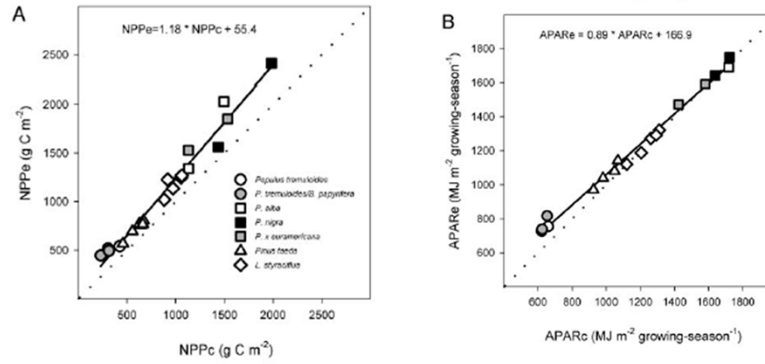
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Summary of CO₂ MetaAnalysis

- Photosynthesis
 - +50% greenhouse, open-top chamber
 - +20-30%: FACE, growth chamber
- Stomatal Conductance
 - -10%
- Biomass
 - +28%

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Forest Response to Elevated CO₂ is Conserved over Range of NPP



Norby et al. 2006 PNAS

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