

# On how trees die and predictions of global forest mortality



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# DEFINITIONS

- **Mortality**

- No respiration, entropy, brown foliage, no more reproduction, negative cellular stain detection, etc

- **Hydraulic failure**

- The *process* towards threshold, irreversible desiccation, i.e. Percent Loss Conductivity (PLC) of 0-100%, etc.

- **Carbon starvation**

- The *process* by which the maintenance of metabolism or defense fails due to limited fuel supply from photosynthesis and stores.
- Law of mass balance

# DEFINITIONS

- **Carbon starvation continued**

- Law of mass balance

Respiration + turgor + defense = photosynthate + available stores + autophagy - growth



Survival

# DEFINITIONS

- **Carbon starvation continued**

- Law of mass balance

Respiration + turgor + defense = photosynthate + available stores + autophagy - growth

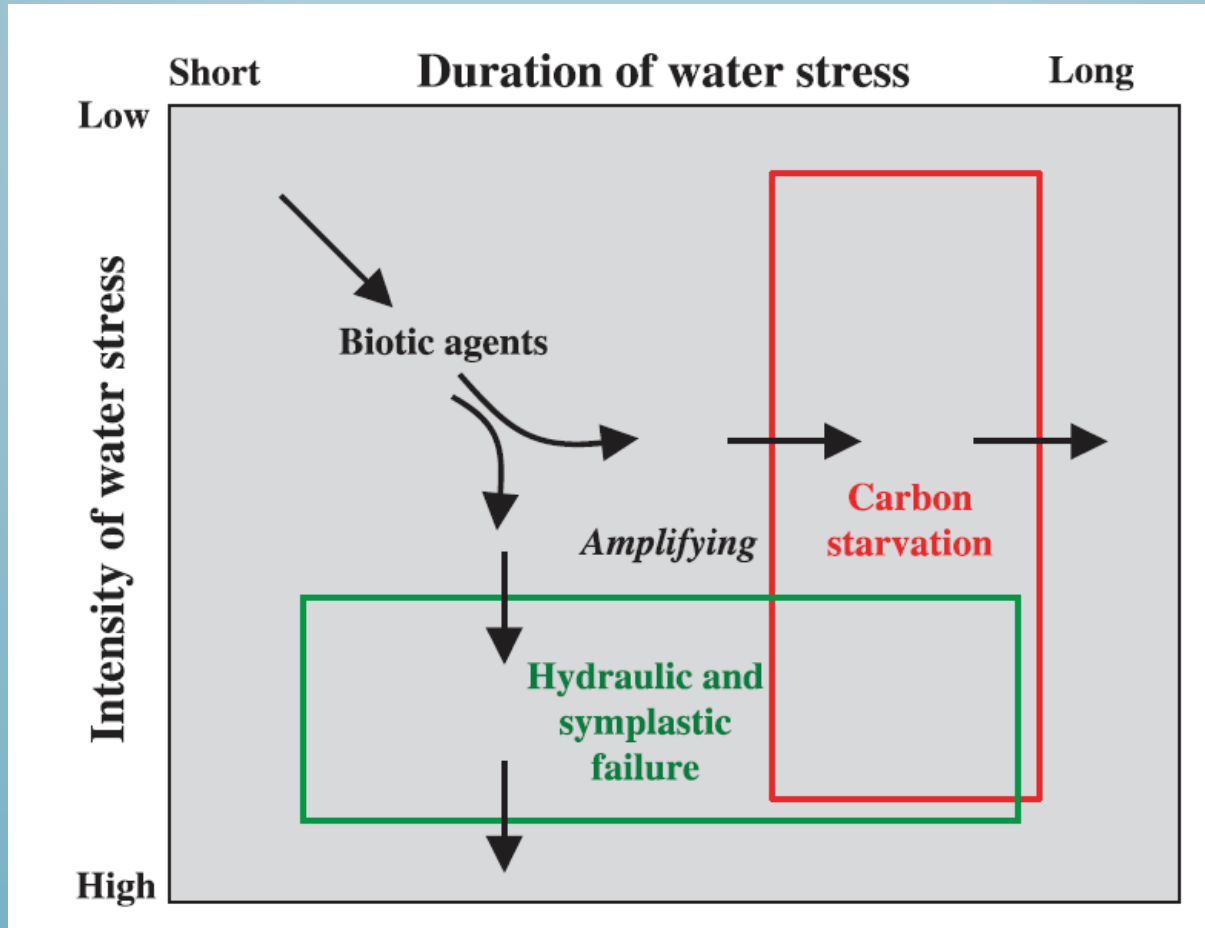


Survival

**I do not consider the hydraulic theory in conflict with existing sink-source theory**

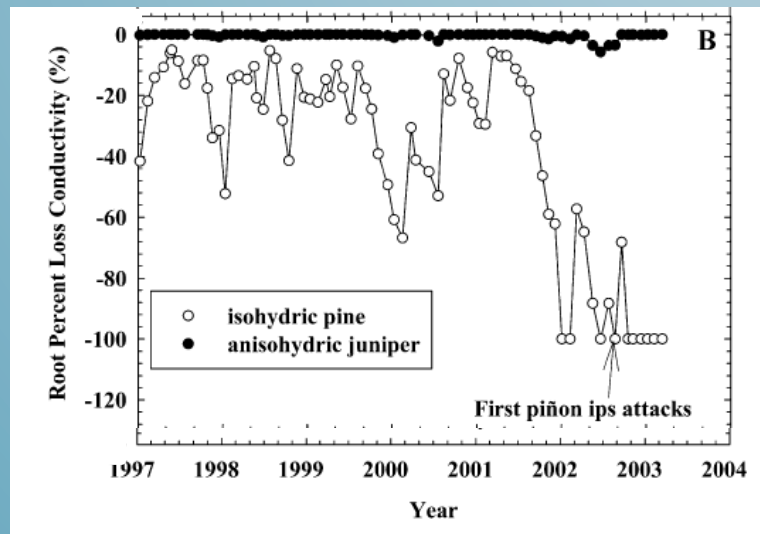


# THE HYDRAULIC FRAMEWORK

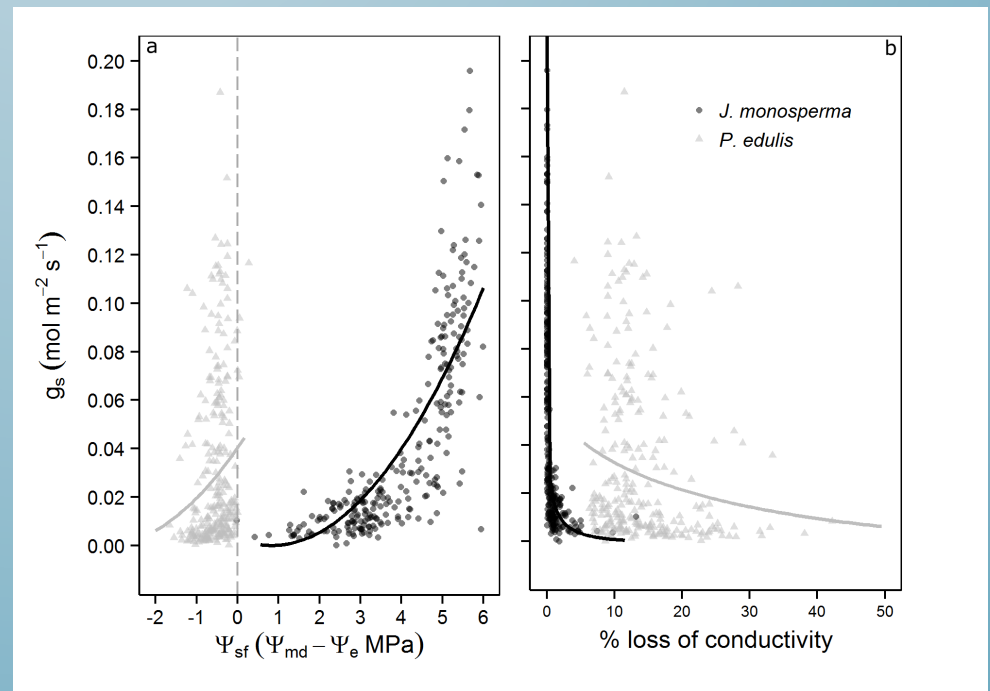


# FALSE DICHOTOMIES: GOOD FOR SCIENCE; BAD FOR SCIENCE

McDowell et al. 2008 predicted relatively anisohydric species were more likely to experience hydraulic failure than relatively isohydric species. This is incorrect. **False dichotomies are useful but dangerous.**



McDowell 2011



Garcia-Forner et al. 2015

# THE SOURCE/SINK DEBATE IS A FALSE DICHOTOMY

THE SOURCE/SINK DEBATE  
IS A FALSE DICHOTOMY

AND

I DO NOT CONTEND THAT ALL PLANTS DIE OF A SPECIFIC  
MECHANISM.

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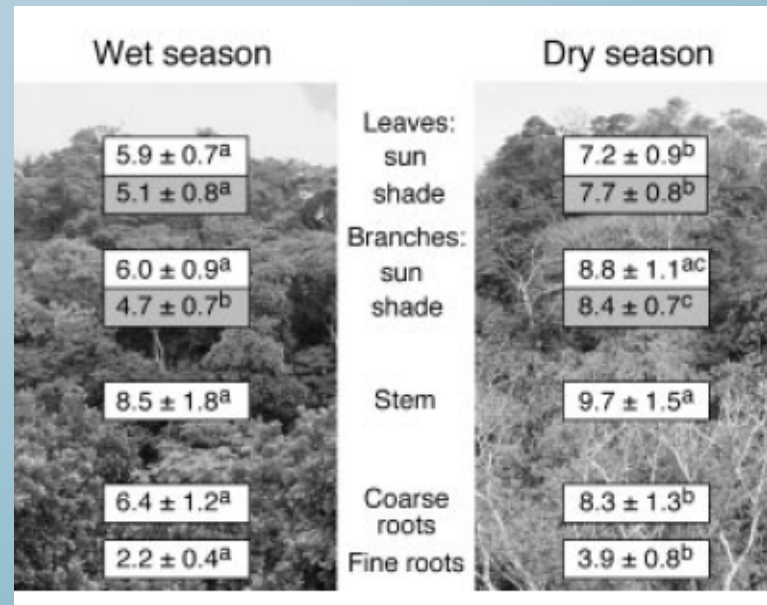
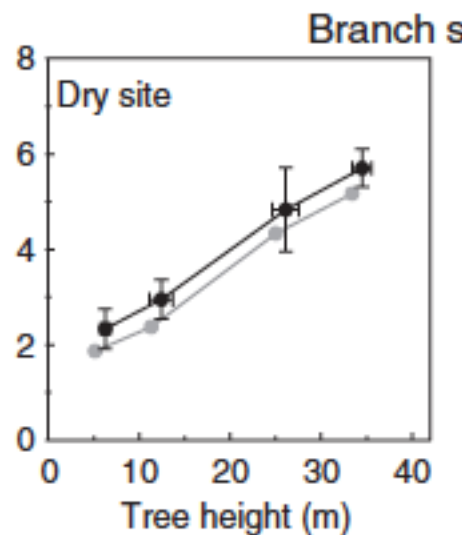
I DO NOT CONTEND THAT ALL PLANTS DIE OF A SPECIFIC  
MECHANISM.

AND

I DO CONTEND THE HYDRAULIC FRAMEWORK PREDICTS THE  
RANGE OF MECHANISMS OF DROUGHT-INDUCED MORTALITY

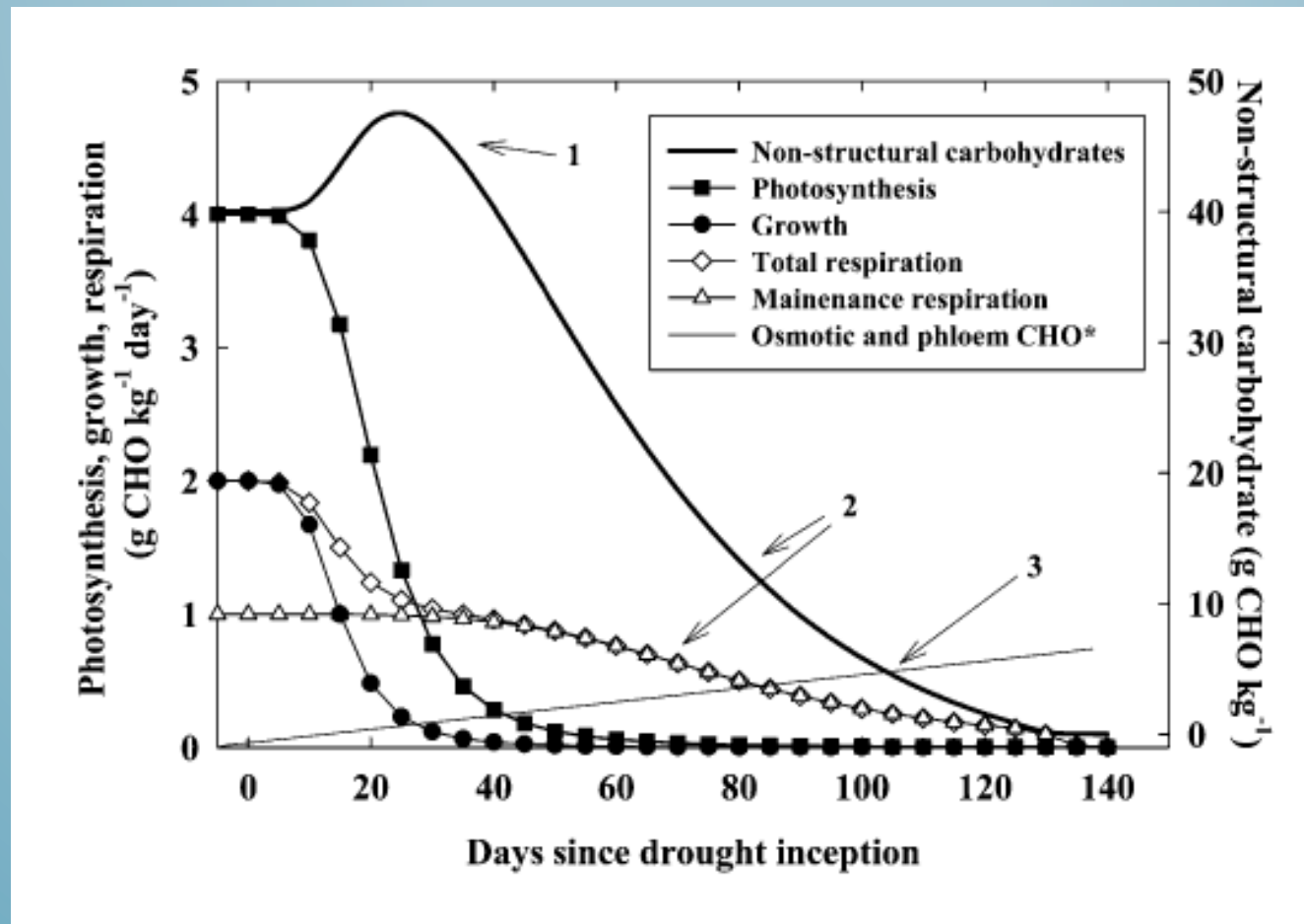
# DEBATE: DROUGHTED PLANTS OFTEN HAVE MORE CARBON THAN WATERED PLANTS

Non-structural carbohydrate concentrations (% dry matter)



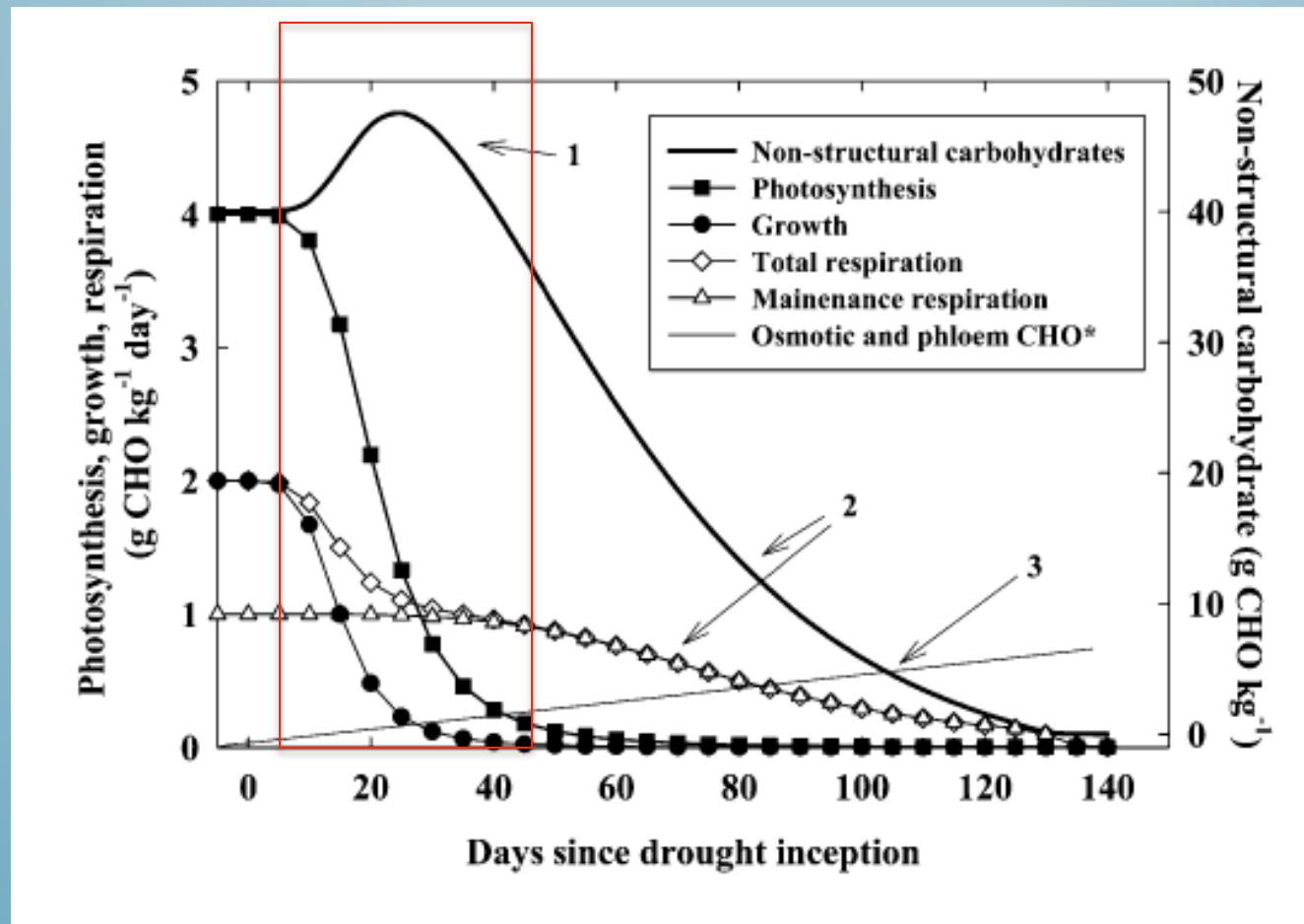


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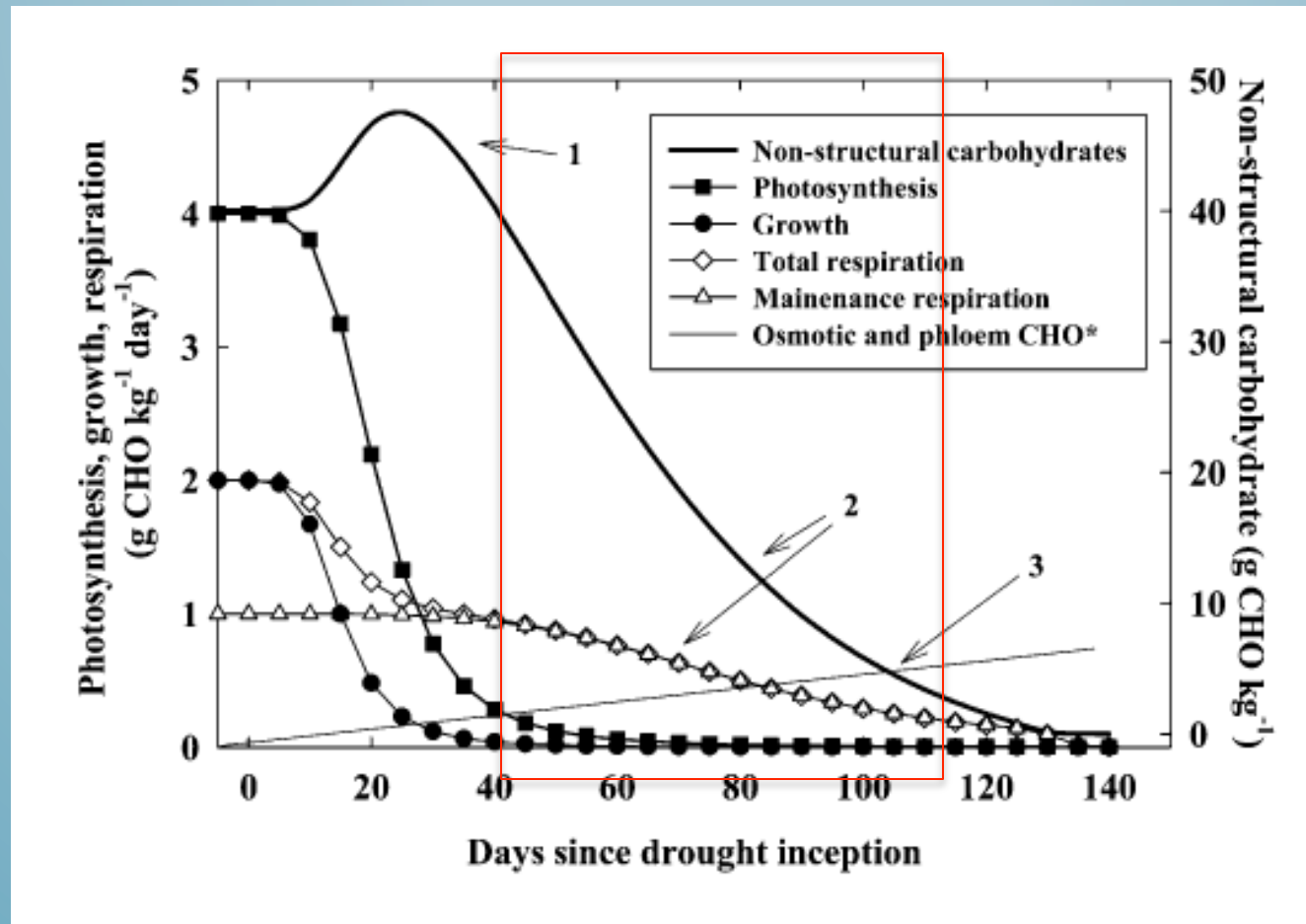
McDowell 2011, lots of other publications demonstrating this, starting with Hsiao

# SINK STRENGTH DECLINES MORE THAN PHOTOSYNTHESIS



McDowell 2011, lots of other publications demonstrating this, starting with Hsiao

# AS SOURCE DECLINES, SINK REMAINS INVOLVED IN THE CARBON BALANCE (RESPIRATION, TURGOR)

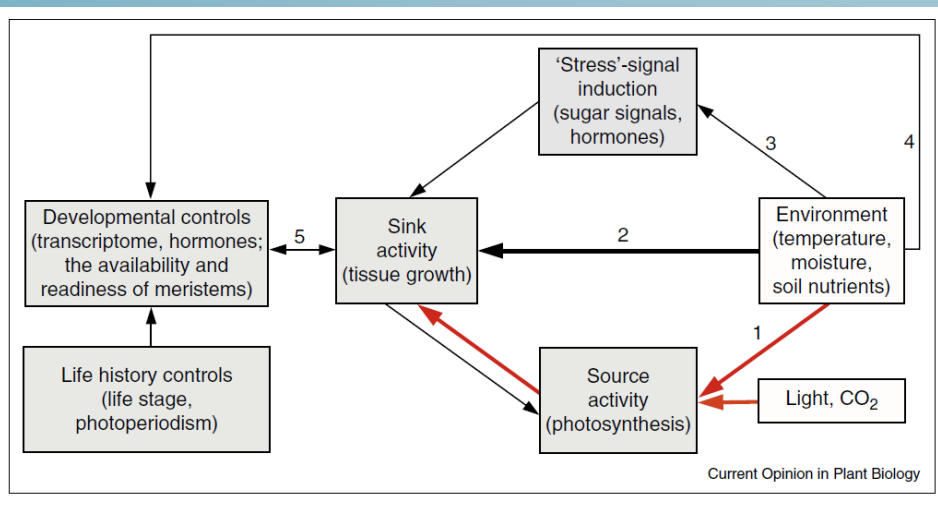
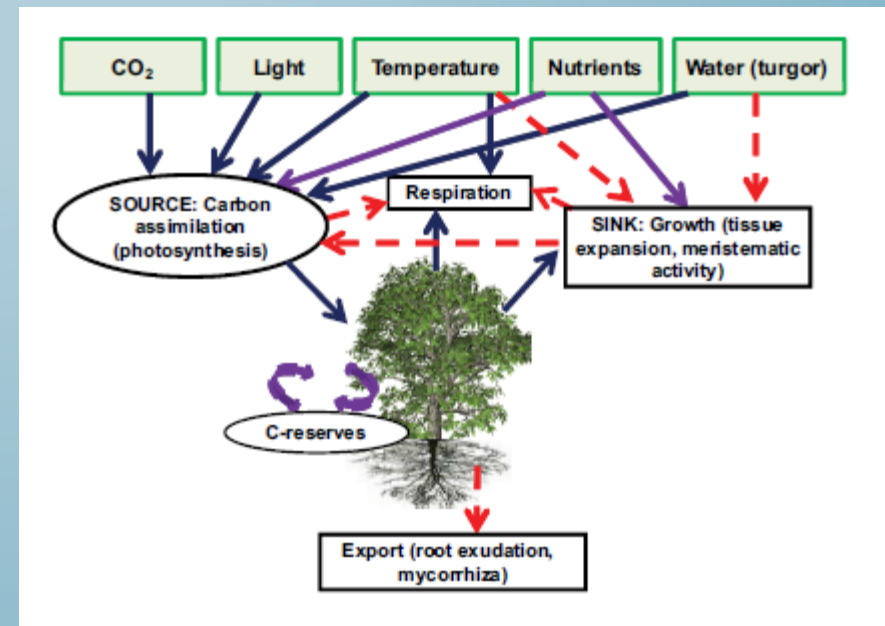
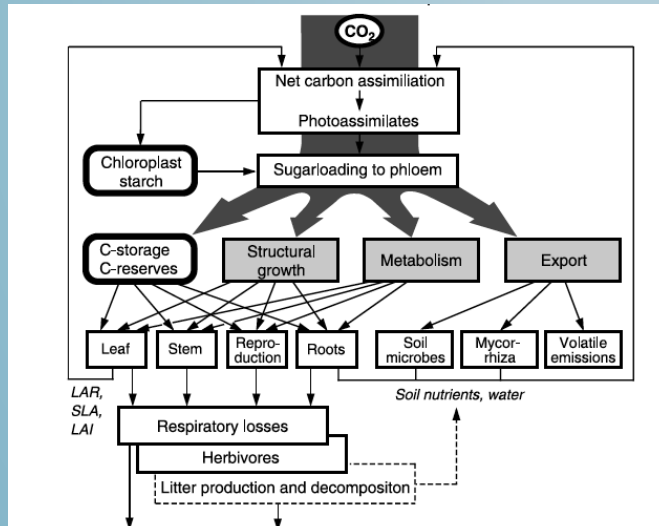


McDowell 2011, lots of other publications demonstrating this, starting with Hsiao

**Important:** studies of stress without mortality are largely irrelevant to understanding how trees die!

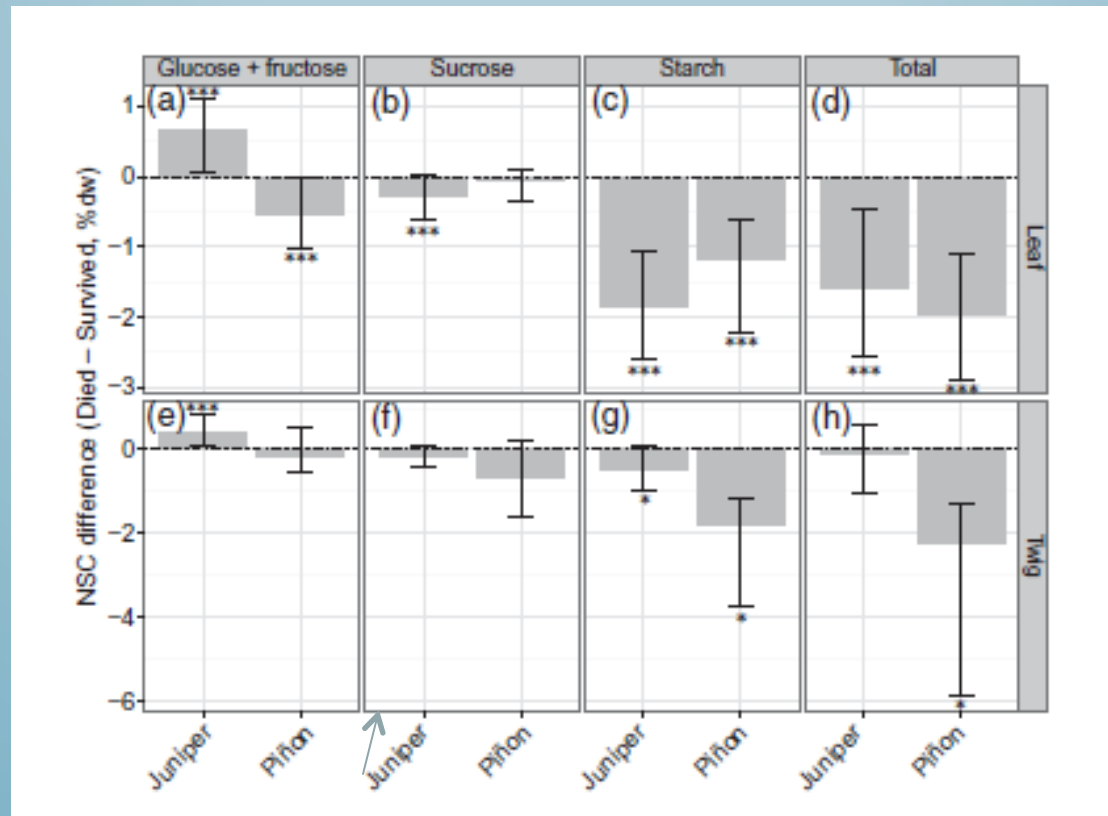
We must kill trees to study mortality.

# SOURCE VS SINK CARBON DYNAMICS IS A FALSE DICHOTOMY. LET'S SIMULATE THE SINK AND SOURCE SYSTEM.



Körner 2003, Fatichi et al. 2014, Körner 2015

# STUDIES THAT PUSH PLANTS TO DEATH OFTEN SEE REDUCED NSC

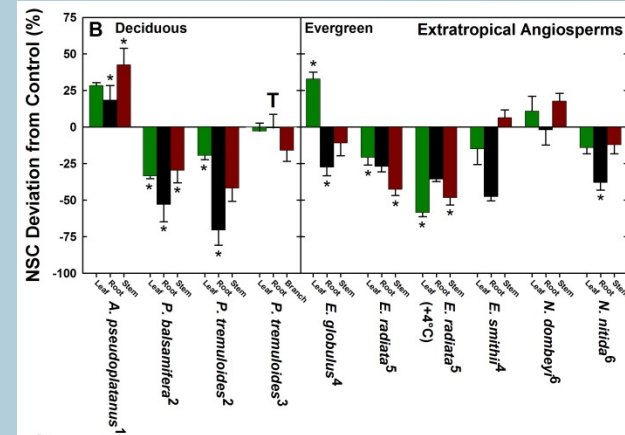


- Consistently low NSC in stressed trees (field study, mature trees)



# EVIDENCE FOR CARBON STARVATION

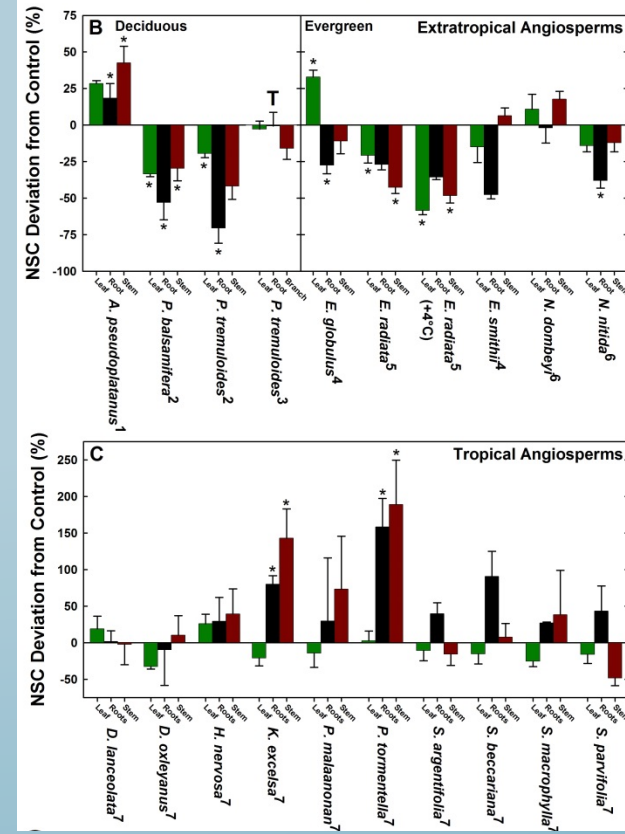
- Extra-tropical angiosperms:



Adams et al. in preparation

# EVIDENCE FOR CARBON STARVATION

- Tropical angiosperms:



Adams et al. in preparation

# EVIDENCE FOR CARBON STARVATION

- Gymnosperms:

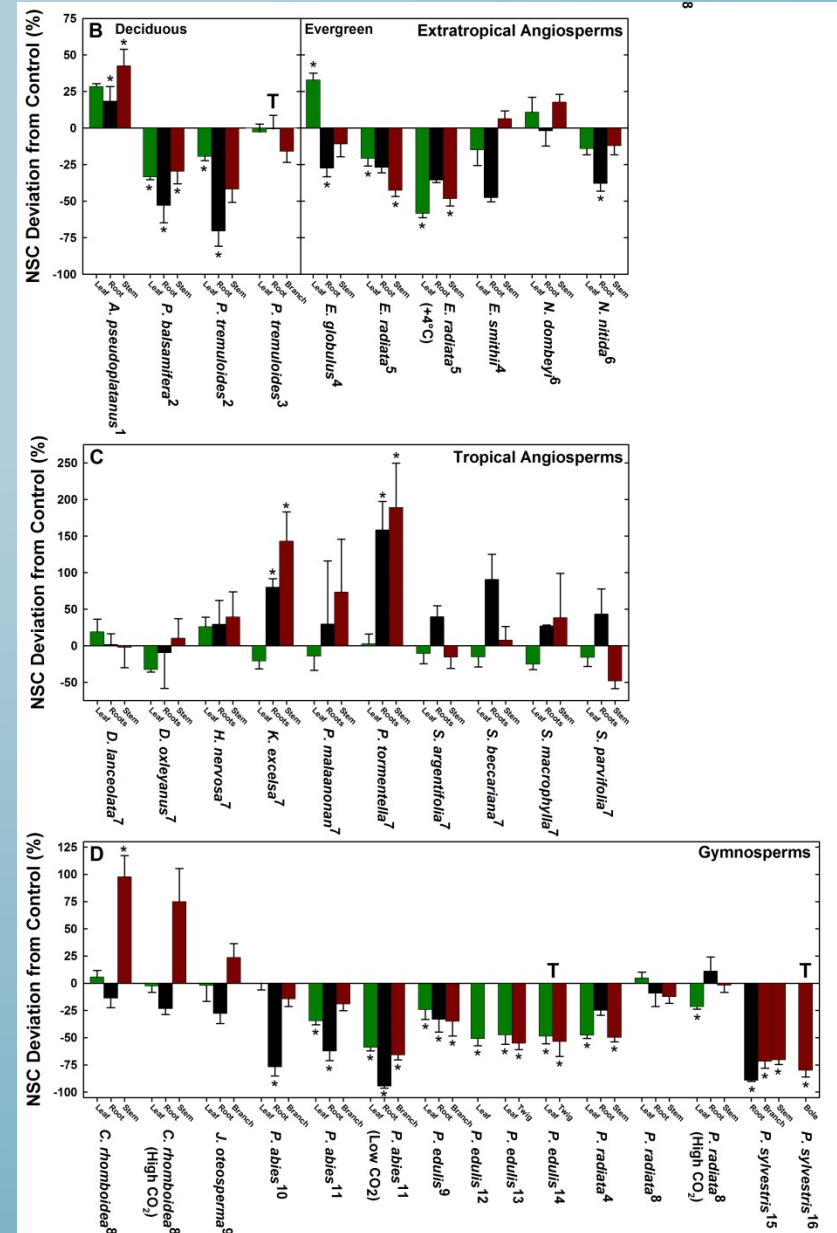
- Overall:

~50% had depleted NSC at death

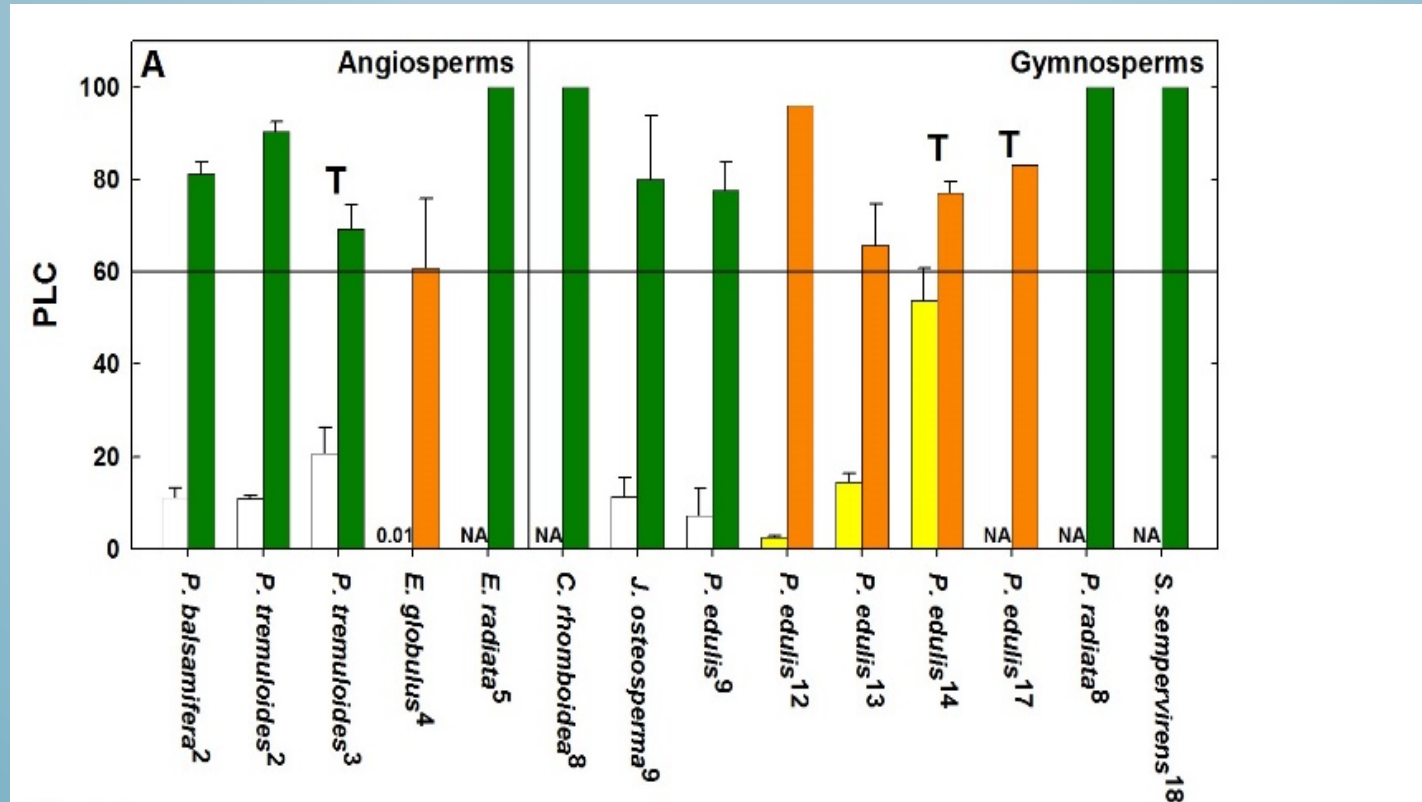
~25% had higher NSC at death

~25% had no NSC change at death

Adams et al. in preparation



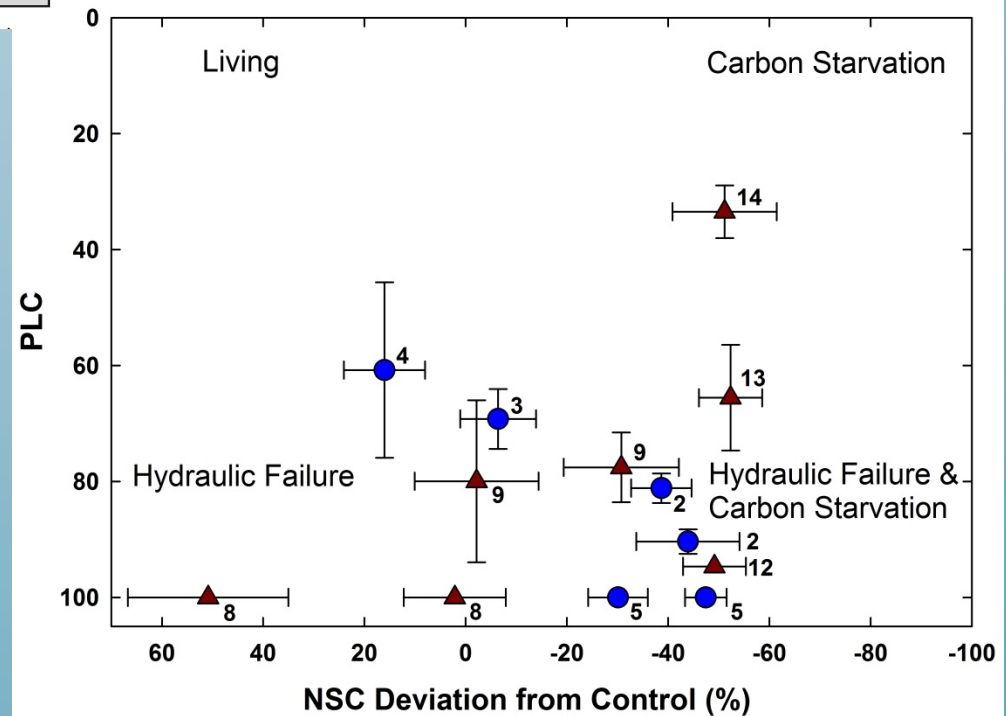
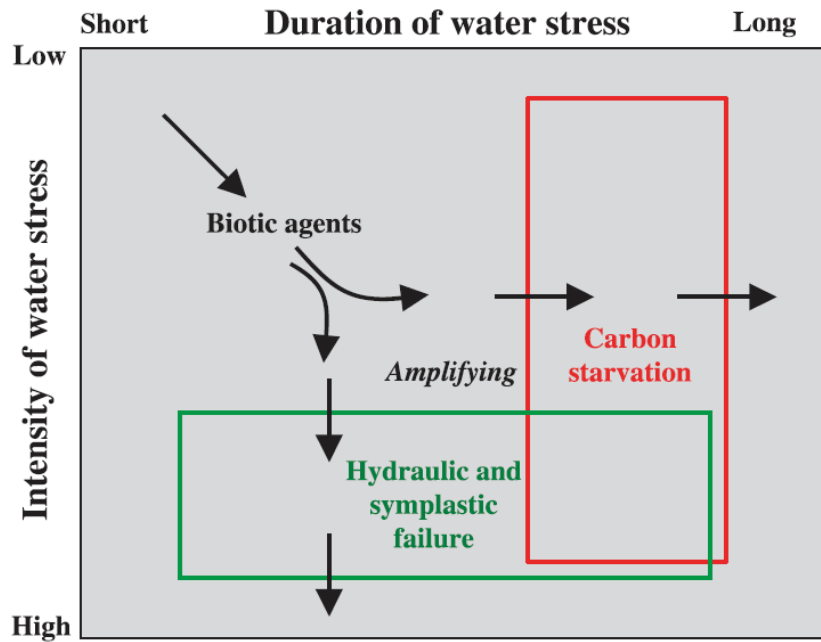
# EVIDENCE FOR HYDRAULIC FAILURE



- Consistent global evidence of high conductivity loss preceding mortality

Adams et al. in preparation

# COMPARISON OF THE HYPOTHESIS TO THE DATA

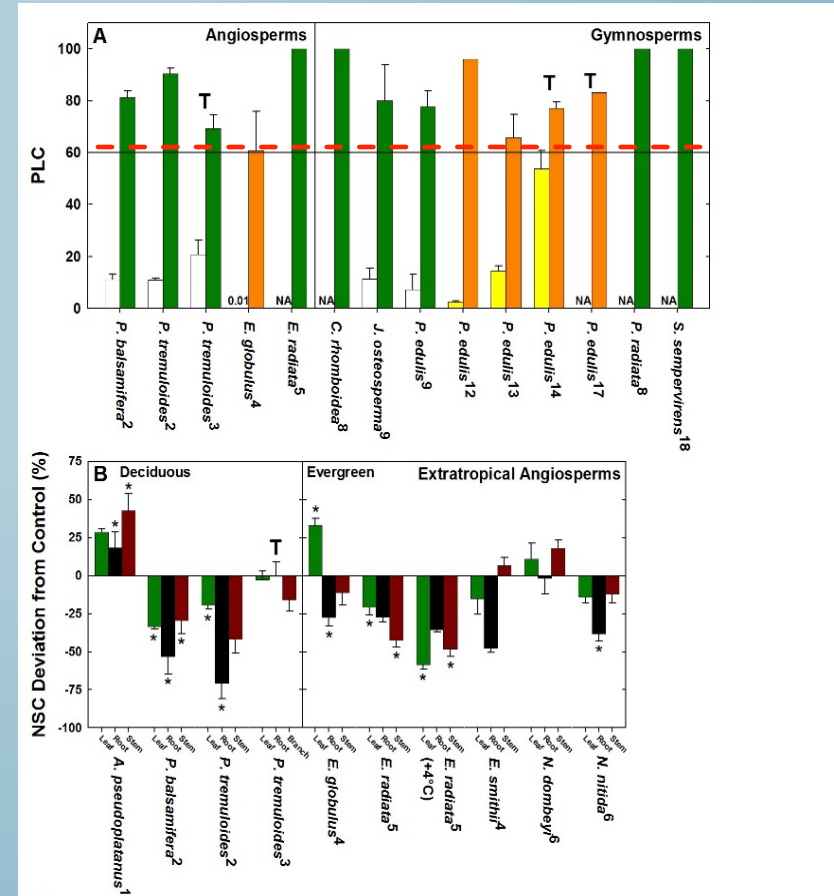


# PROBLEMS WITH THE EVIDENCE FOR CARBON STARVATION AND HYDRAULIC FAILURE

- PLC and NSC thresholds unknown
- Cellular NSC availability unknown

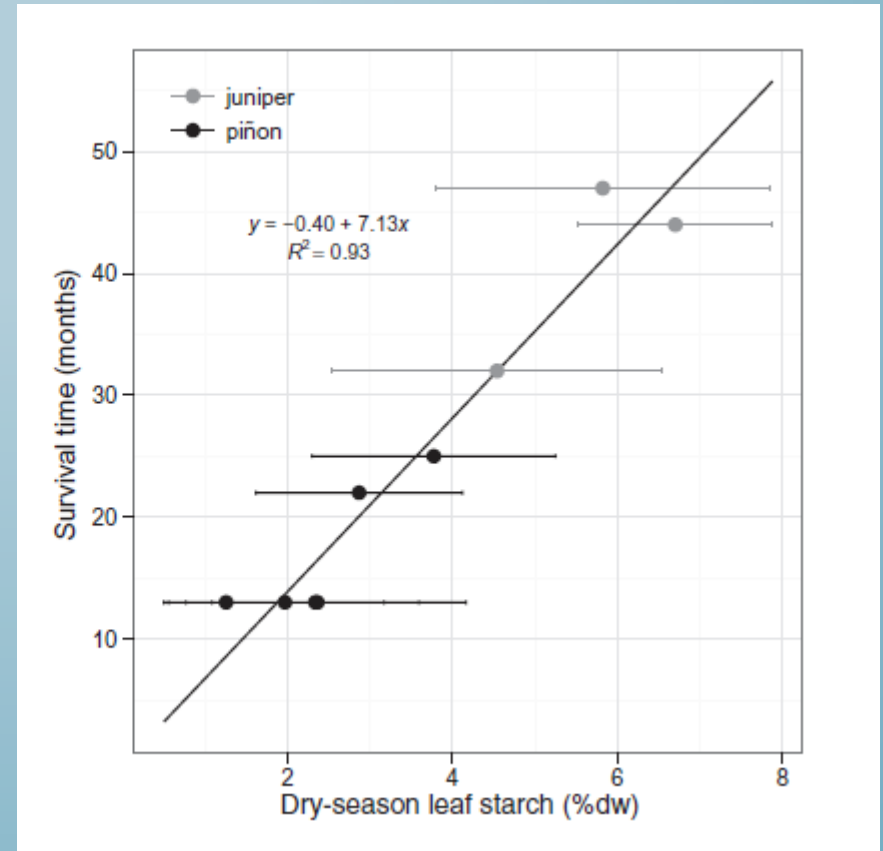
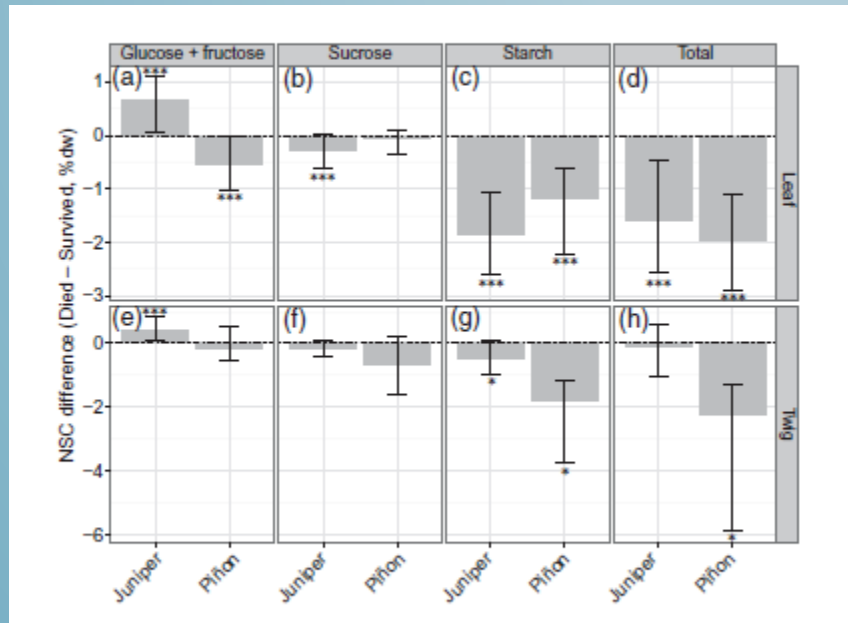
NOTE: Sustained PLC >60% associated with mortality (McDowell et al. 2013, Sperry and Love 2015, Anderegg et al. 2015)

Dashed horizontal line





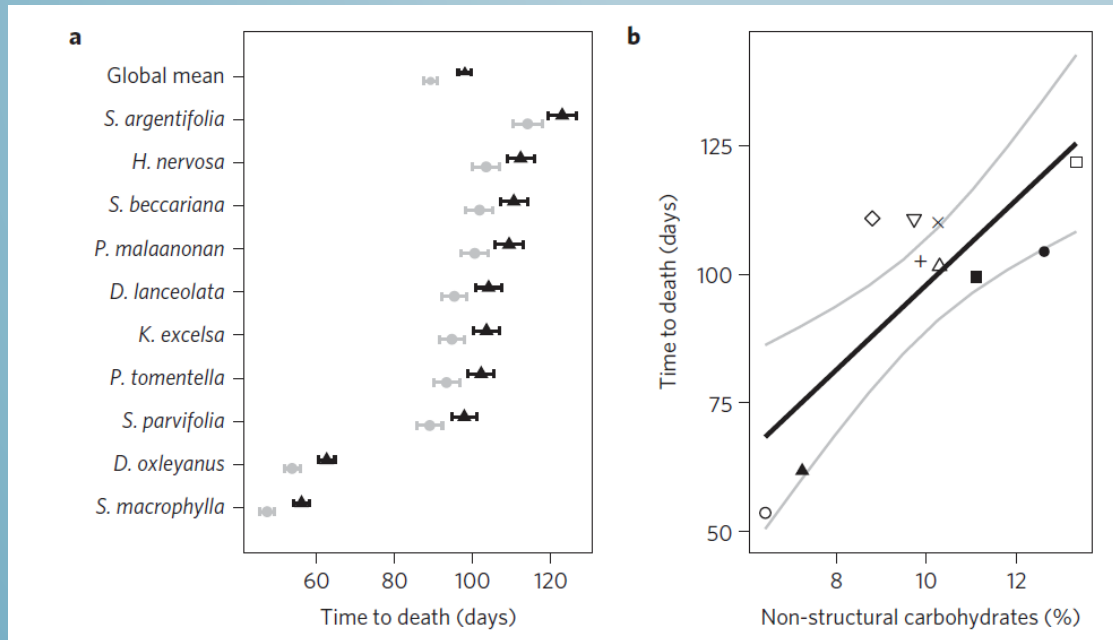
# NSC IS *CORRELATED* WITH SURVIVAL



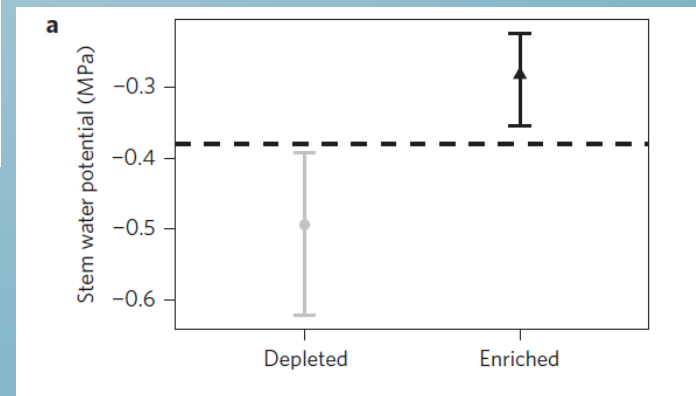
- Consistently low NSC in stressed trees
- Also see Sevanto et al. 2014 for clear evidence

Dickman et al. 2014

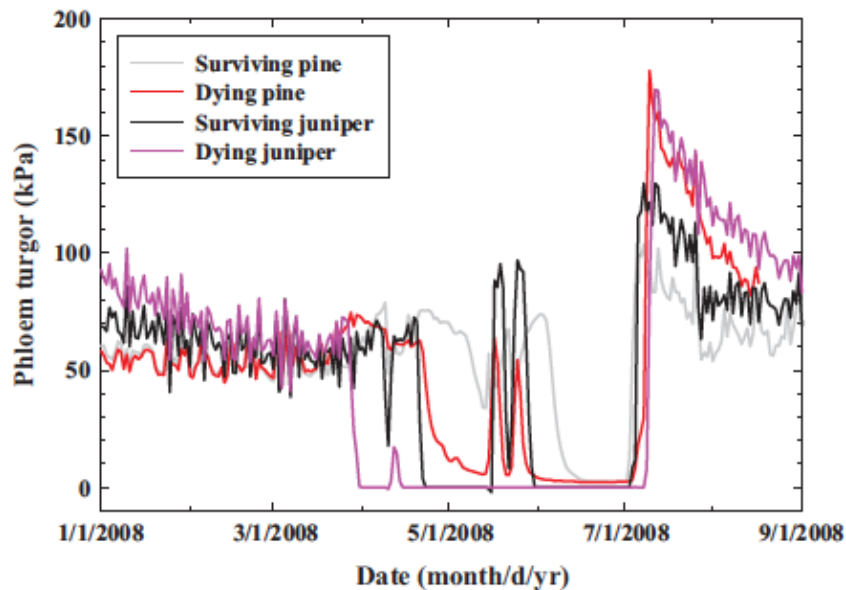
# NSC MANIPULATIONS DEMONSTRATE THE RELATION BETWEEN NSC AND SURVIVAL IS POSSIBLY CAUSAL.



And NSC may influence hydraulics, as expected

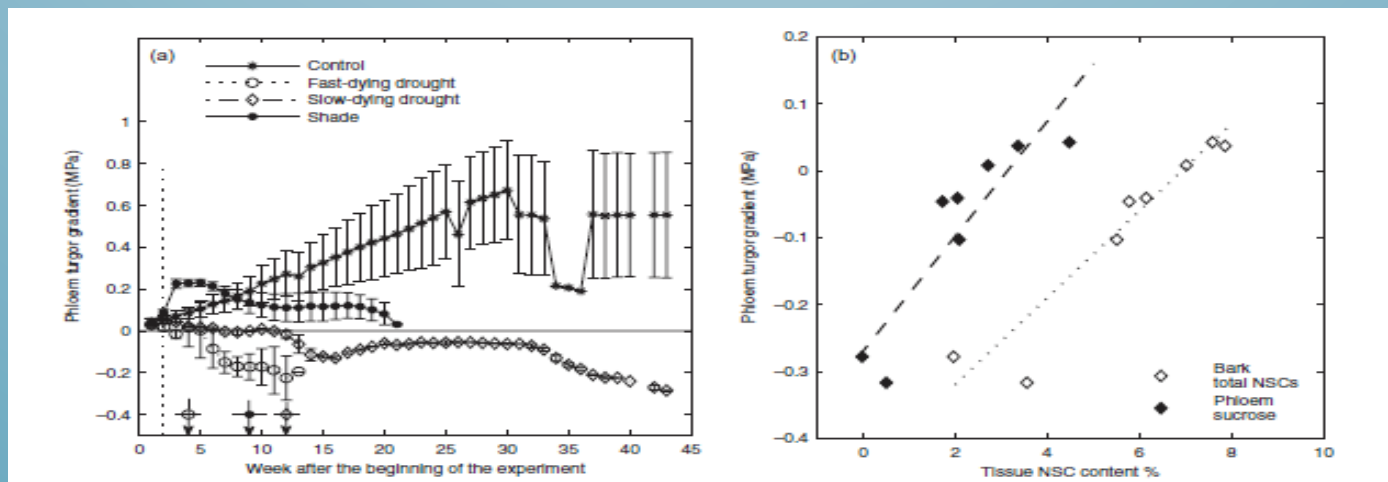


# PHLOEM TRANSPORT FAILURE SHOULD ACCELERATE STARVATION AND HYDRAULIC FAILURE



- Simulations and observations of phloem function failure proceeding mortality

McDowell et al. 2013; Sevanto et al. 2014

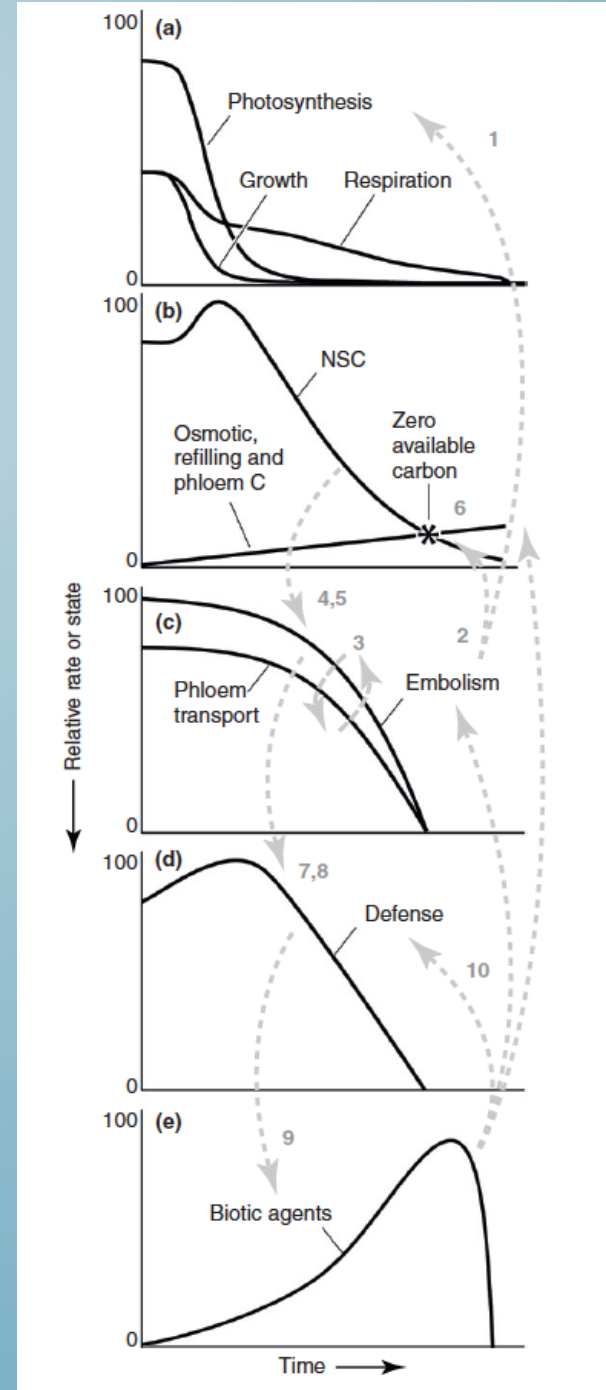


SHOULD WE EXPECT THE  
HYDRAULIC FRAMEWORK TO  
PREDICT ALL DROUGHT-  
ASSOCIATED MORTALITY?

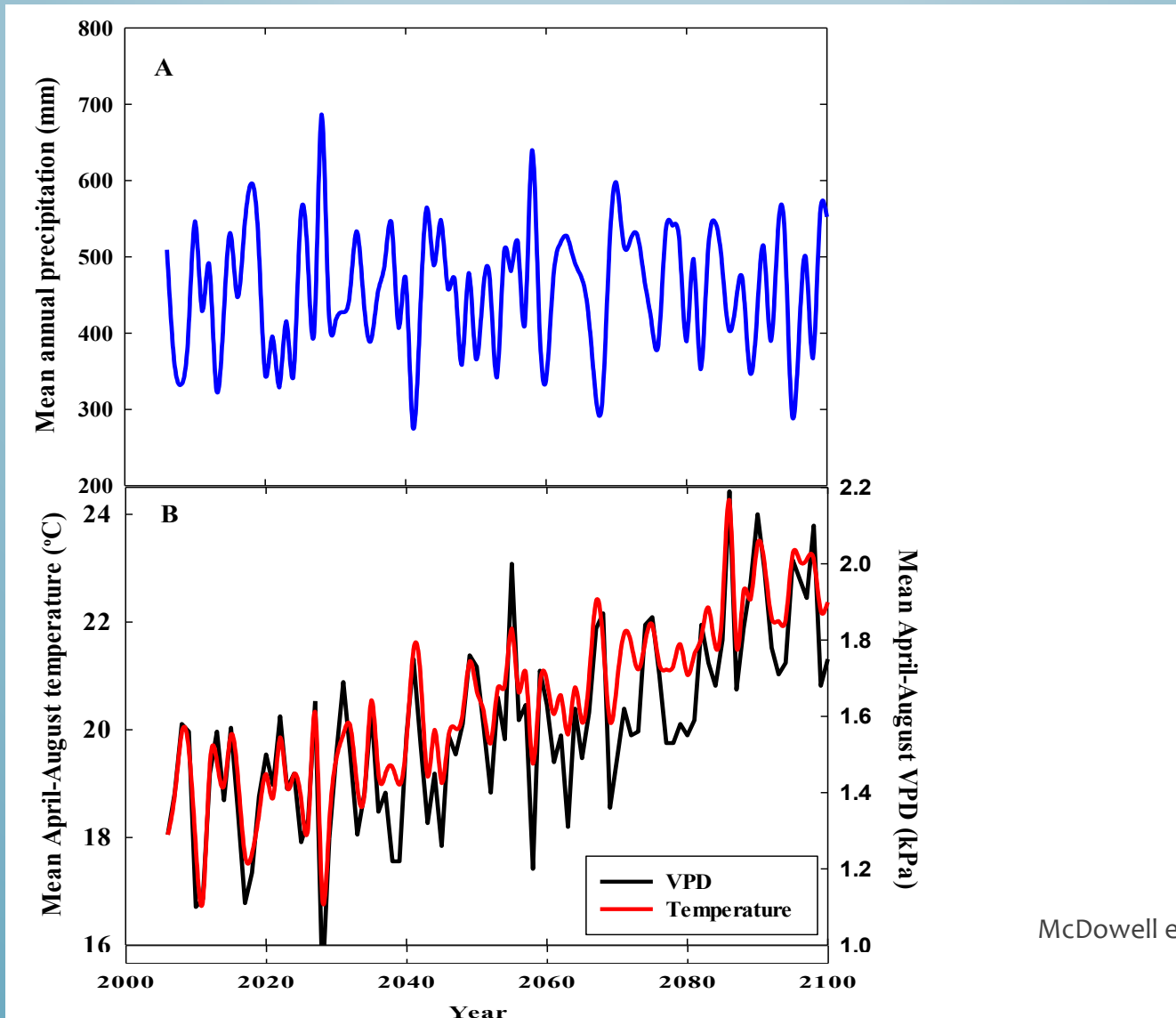
SO FAR, THE EVIDENCE  
SUPPORTS THIS.

BUT THE DETAILS, SEMANTICS,  
AND PROCESSES VARY.

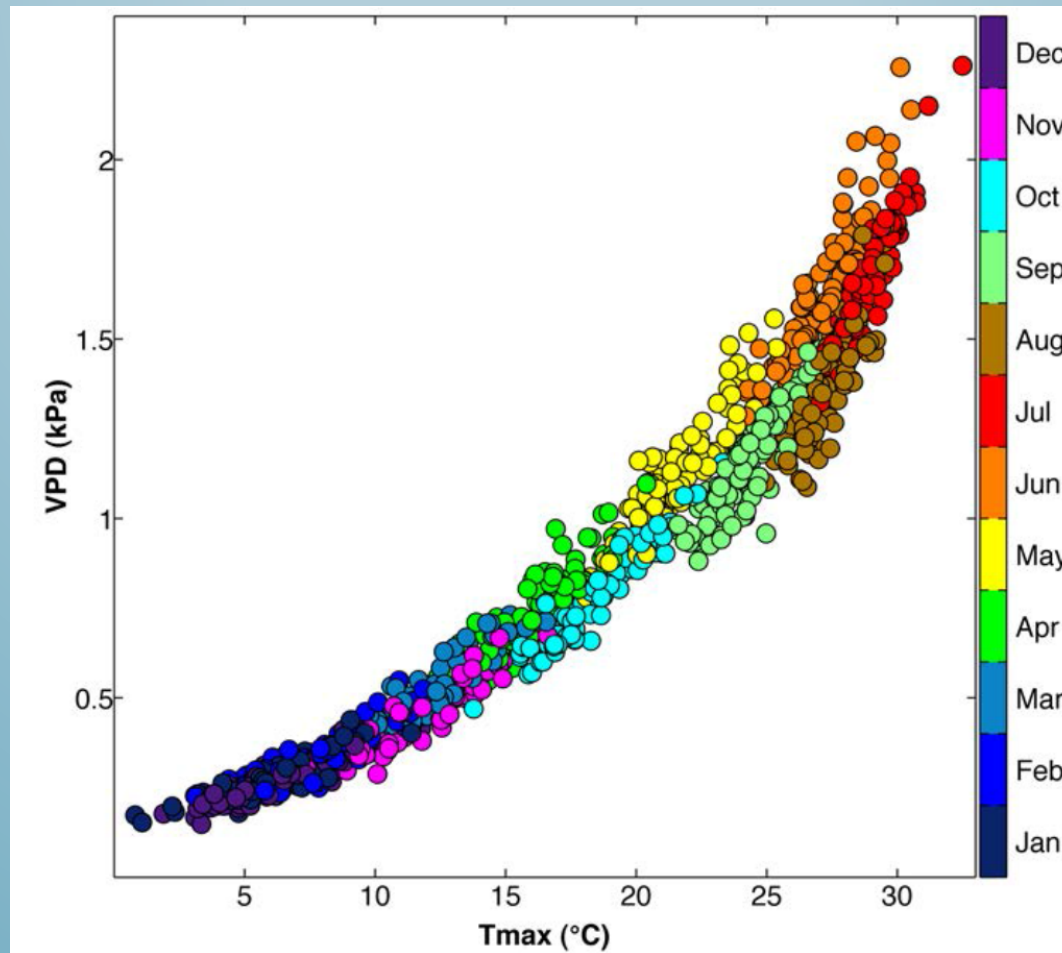
McDowell et al. 2011



Precipitation has always and will always vary.  
What's new is chronic temperature and VPD rise



VAPOR PRESSURE DEFICIT (VPD) GOES UP NON-LINEARLY  
WITH TEMPERATURE (EVEN WITH RISING SPECIFIC  
HUMIDITY!)



Williams et al. 2013

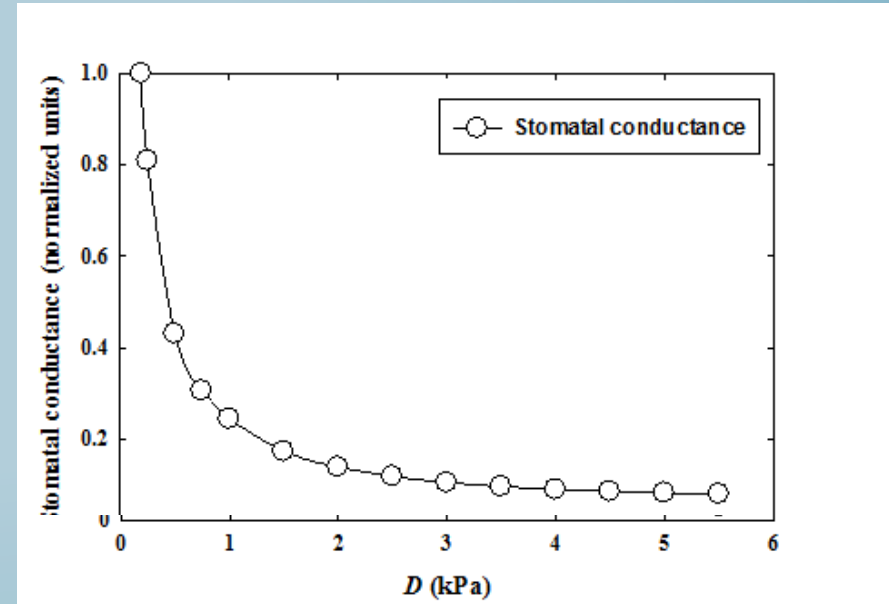


# Theoretical predictions from Darcy's law corollary

Rising VPD = reduced stomatal conductance, unless hydraulic architecture shifts at the ecosystem scale.

$$G = \frac{A_s k_s (\Psi_s - \Psi_l)}{h \eta A_l D}$$

Predictions: reduced tree height and leaf area,  
increased anisohdricity  
= shifts from tall to short plants, and shifts  
from gymnosperms to angiosperms

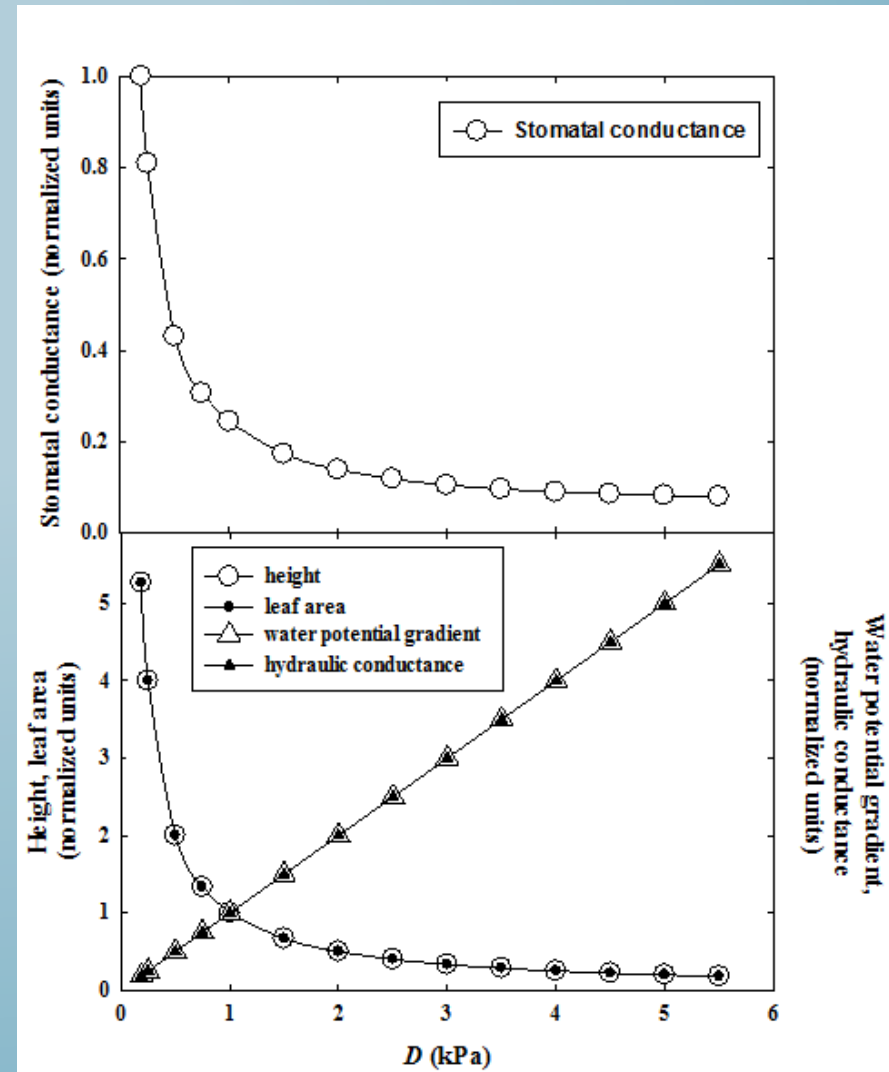


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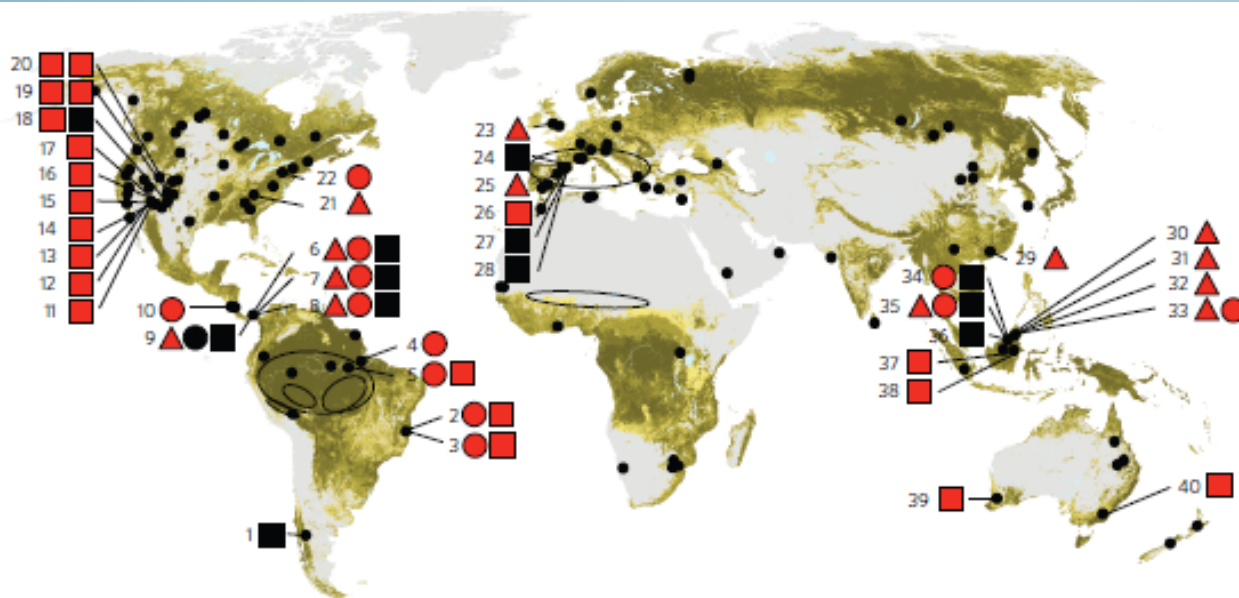
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Predictions: reduced tree height and leaf area, increased anisohydry  
= shifts from tall to short plants, and shifts from gymnosperms to angiosperms



# Larger trees suffer most during drought in forests worldwide

Amy C. Bennett<sup>1,2</sup>, Nathan G. McDowell<sup>3</sup>, Craig D. Allen<sup>4</sup> and Kristina J. Anderson-Teixeira<sup>1,5\*</sup>



**Red symbols:** big trees survive or grow less than small trees in drought

**Black symbols:** big and small trees equivalent

## Darcy's law predicts widespread forest mortality under climate warming

Nathan G. McDowell<sup>1\*</sup> and Craig D. Allen<sup>2</sup>

These global observations are consistent with predictions from hydraulic theory (McDowell and Allen, *Nature Climate Change* 2015).

Climate warming is predicted to exacerbate these drought impacts.

# WE TEST VEGETATION MODELS AGAINST DROUGHT + HEAT EXPERIMENTS

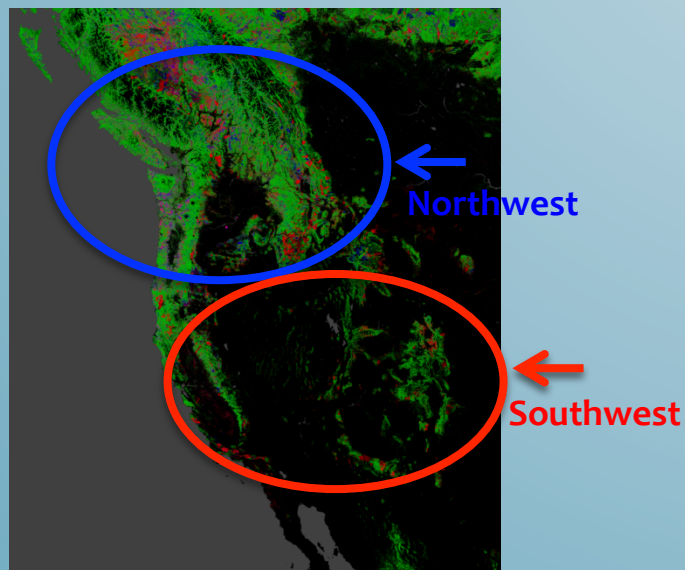


McDowell et al. *New Phytologist* 2013

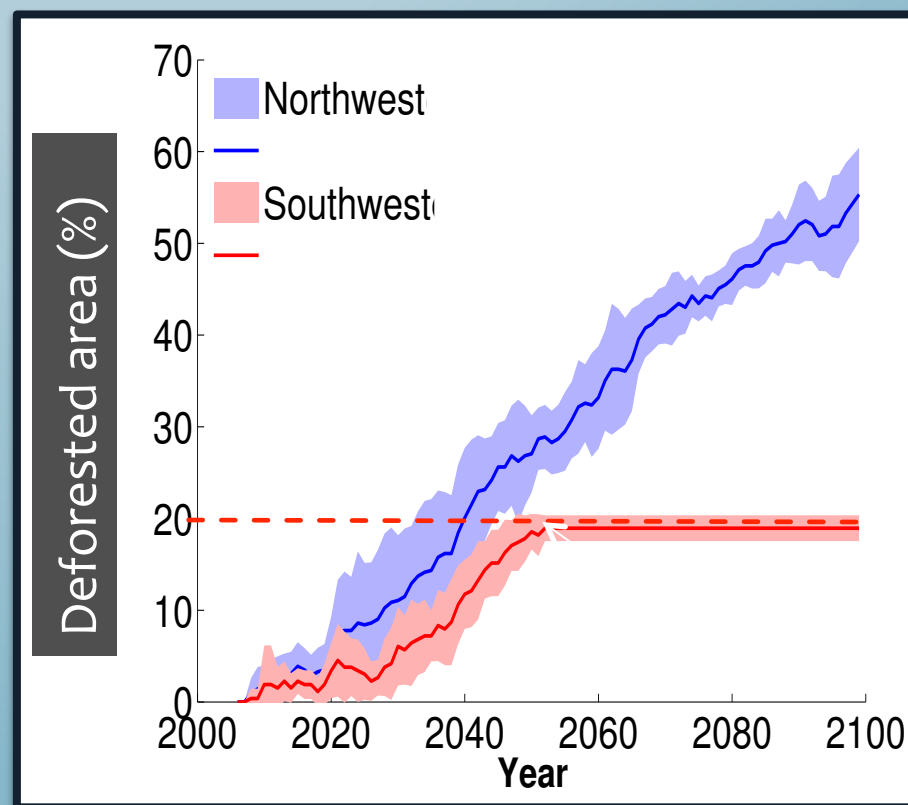




# OUR SIMULATIONS SUGGEST WIDESPREAD FOREST LOSS IN WESTERN USA.

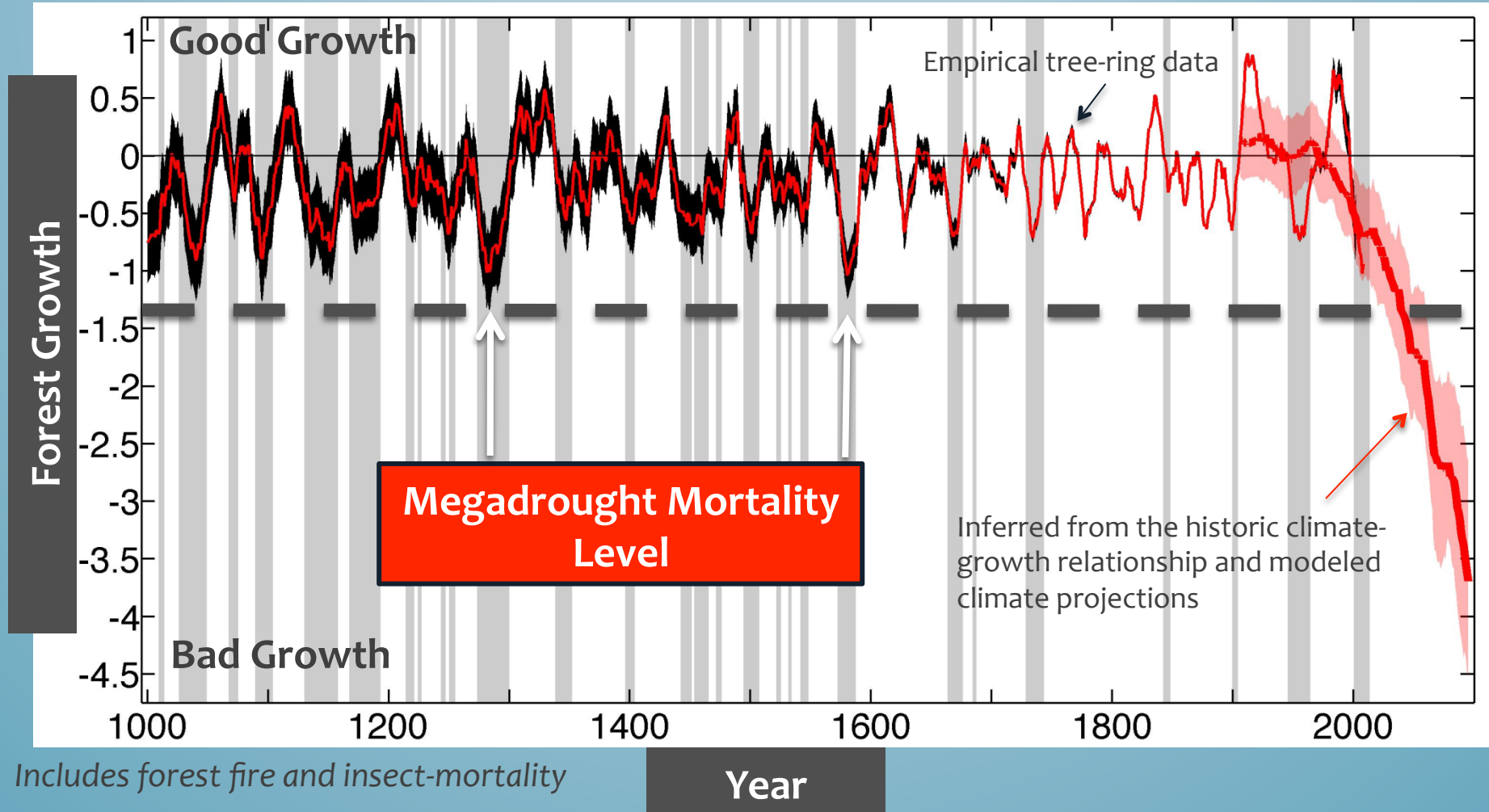


6 Pg C released by 2100  
= 4 years USA fossil fuel emissions  
Does not include wildfire



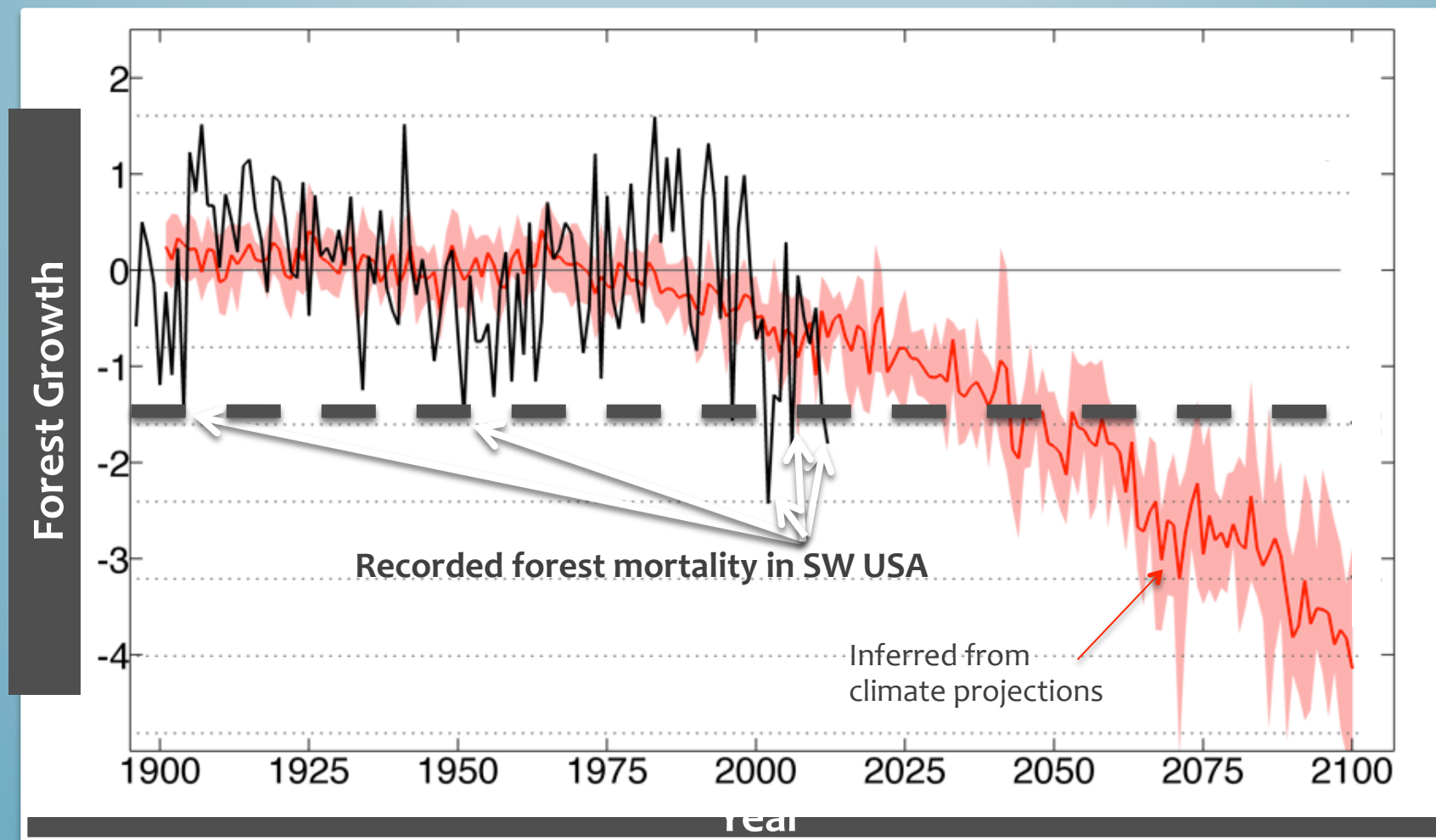
Jiang et al. *J. of Climate*, 2013

# Our tree-ring approach predicts chronic megadrought by 2050 = few surviving forests



Williams et al. *Nature Climate Change*, 2013

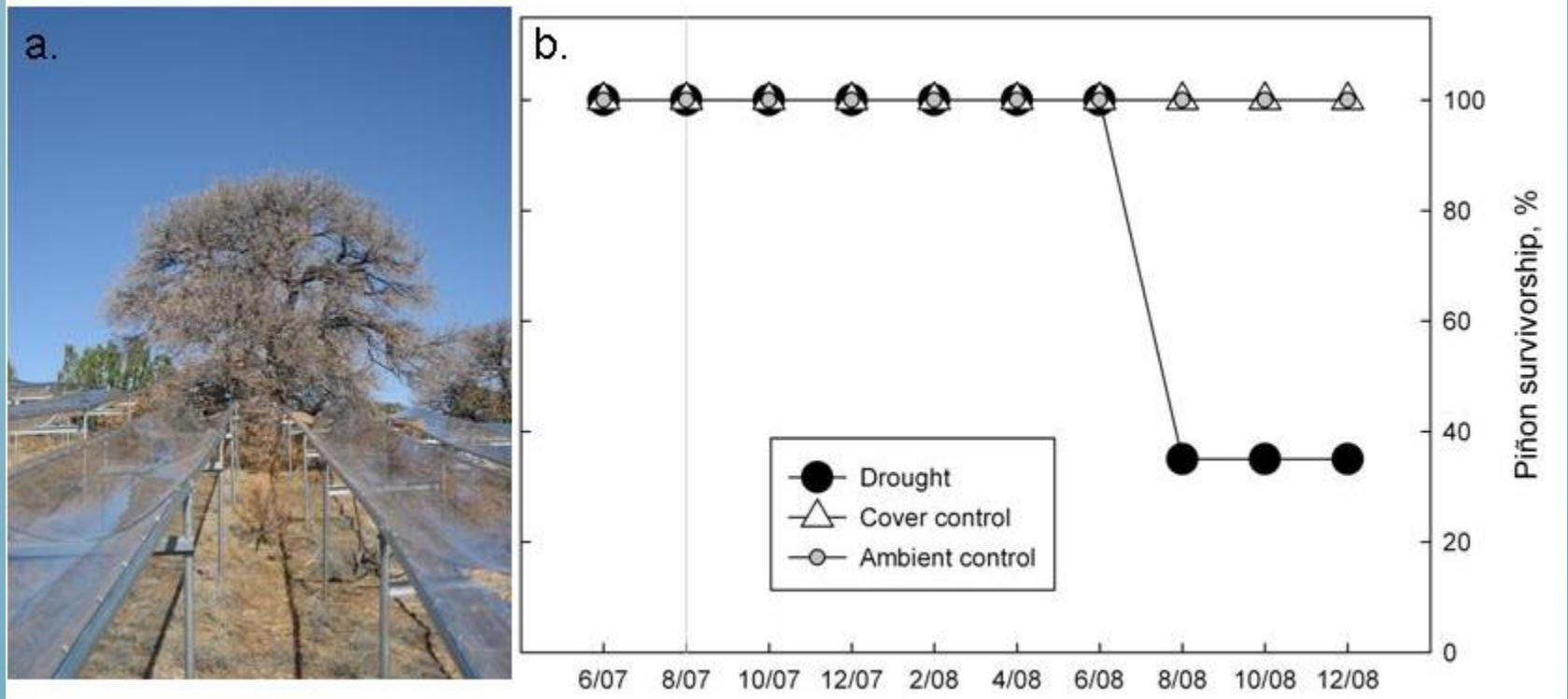
We are already crossing the megadrought threshold  
~30% of SW USA forests have died since 1984



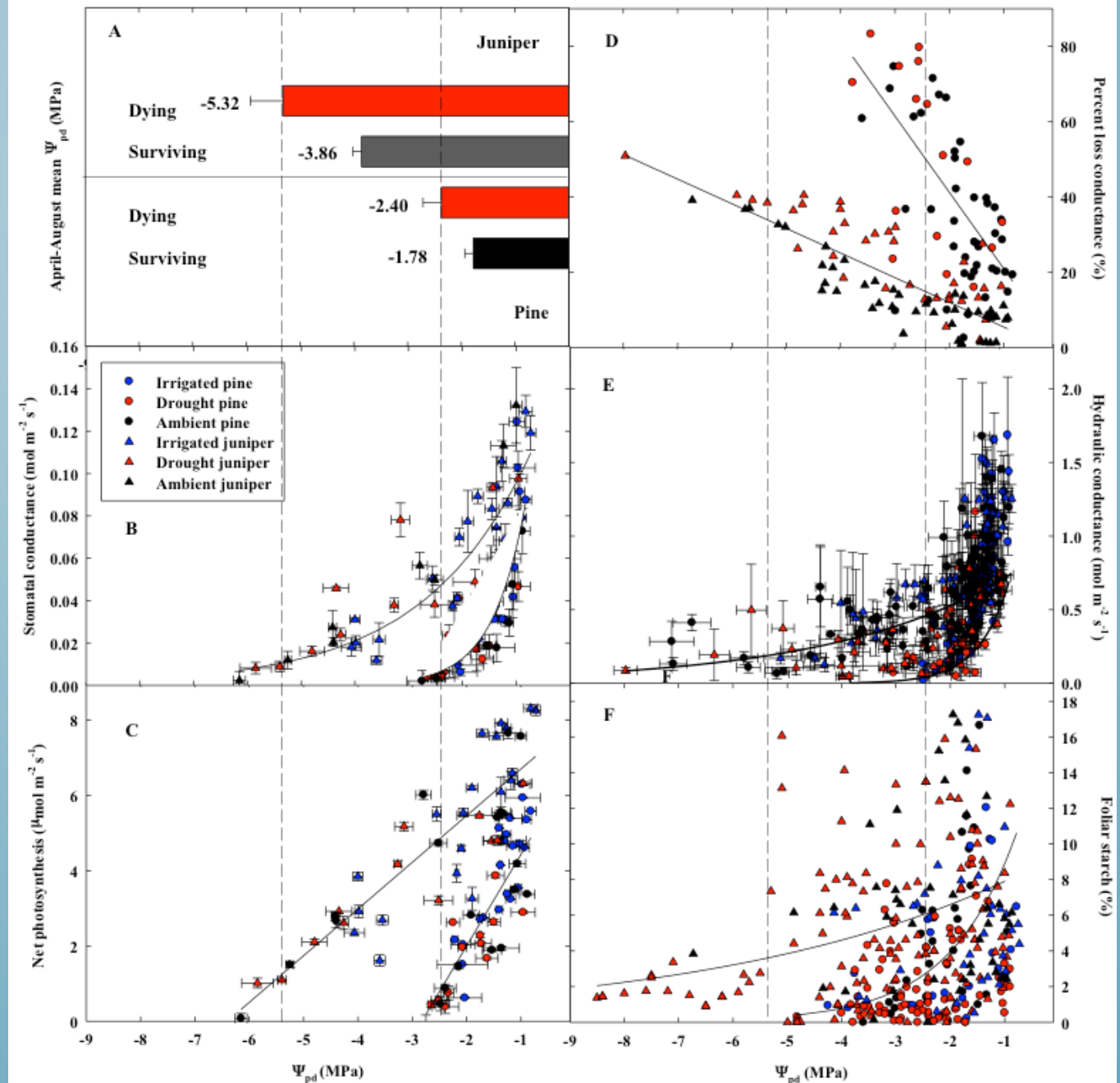


# LETS TEST THIS IDEA WITH SIX VALIDATED MODELS!

FIELD SITE: 8 YEAR, 50% PRECIPITATION REDUCTION IN PINON PINE-JUNIPER WOODLAND



**Key result:**  
consistent water potential thresholds for death and associated mechanisms (carbon starvation and hydraulic failure)



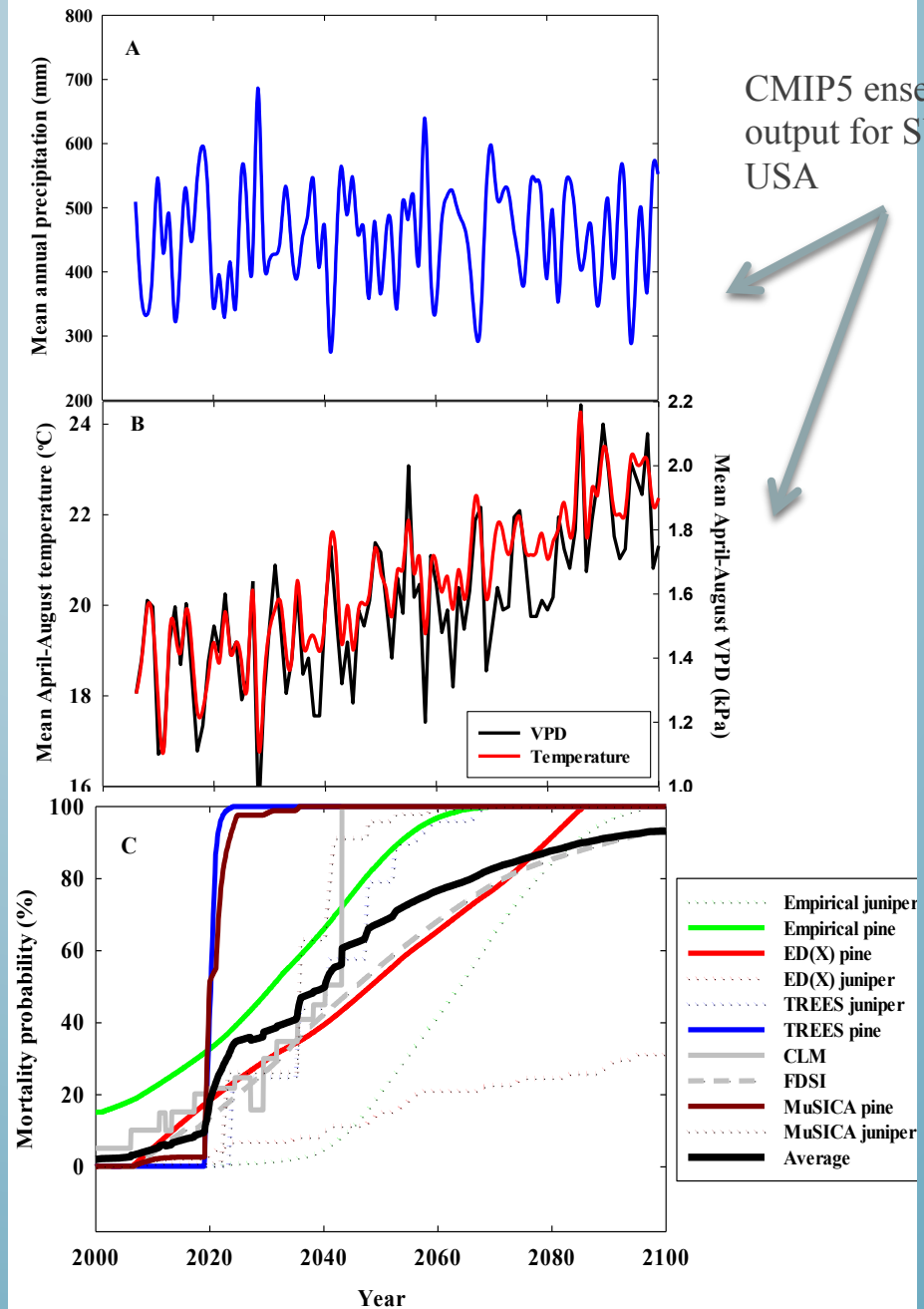
McDowell et al. *Nature Climate Change* in press

Precipitation may not change

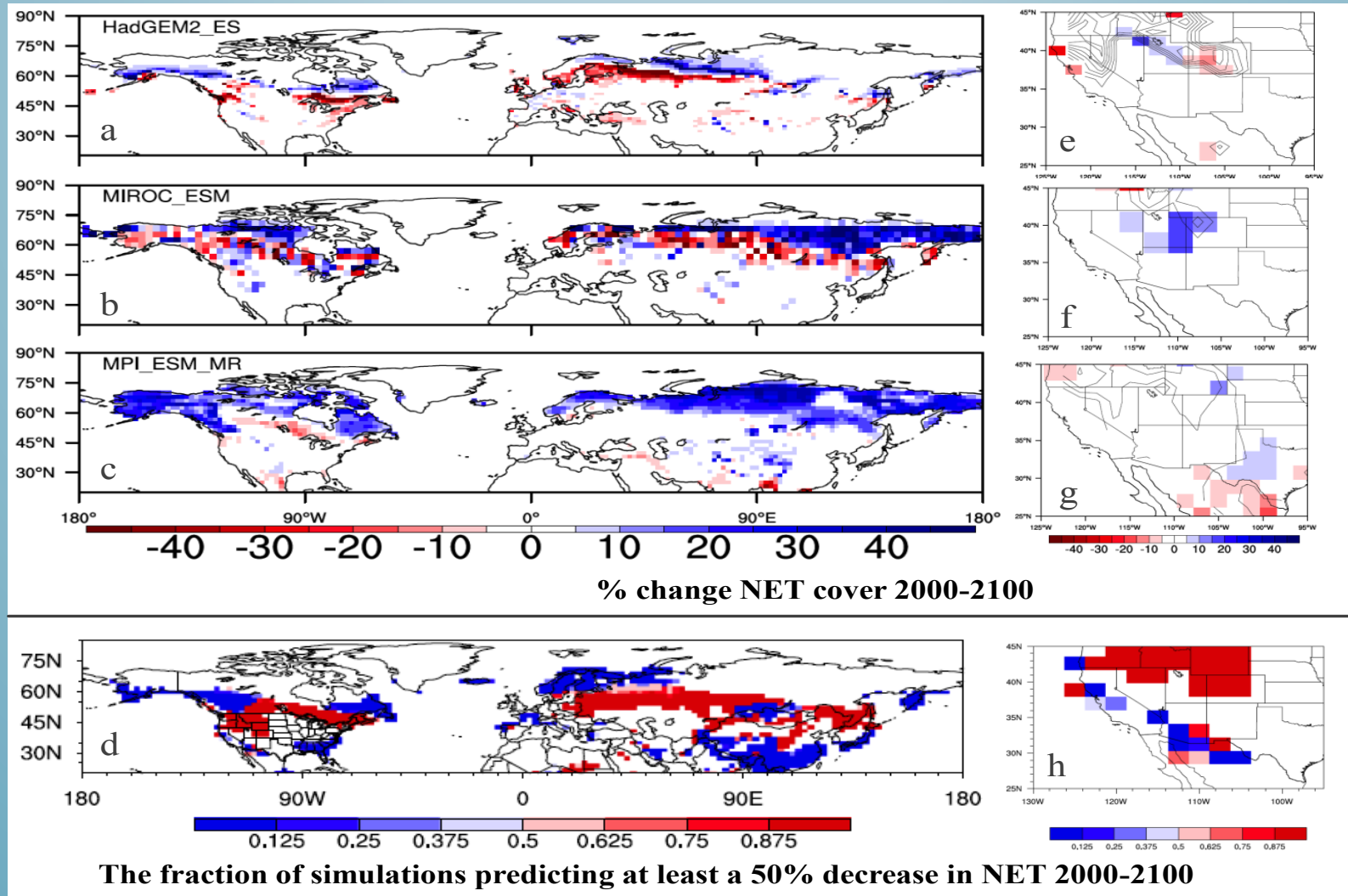
But, temperature and hence VPD is likely to increase

Hence water potential in all six models **crosses mortality thresholds around 2040 for pine, 2060 for juniper.**

McDowell et al. *Nature Climate Change* in press



# CMIP5 AND CESM 3.5 PREDICTIONS ARE CONSISTENT WITH SW USA PREDICTIONS (BUT NOTE REGIONAL ERROR)



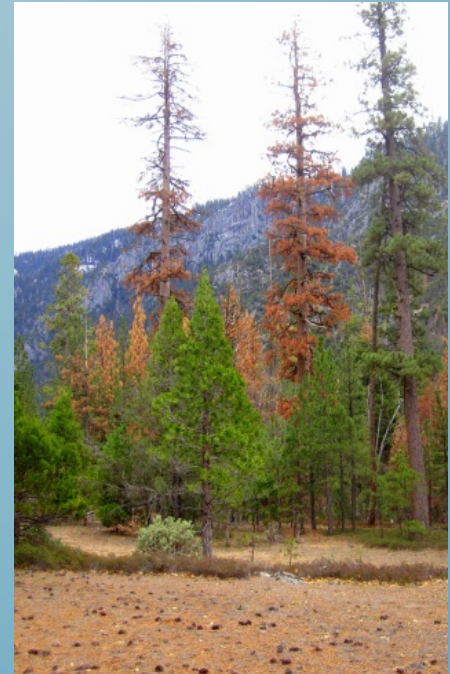


# CONCLUSIONS

- 1) Source vs sink carbon dynamics is a false dichotomy; growth and mortality process are not that simple.
- 2) The carbon starvation hypothesis does not challenge nor disagree with sink driven growth.
- 3) All approaches have error and assumptions. We need many approaches to build reliable predictions.
- 4) Using all available data, predictions for temperate conifers are dire.

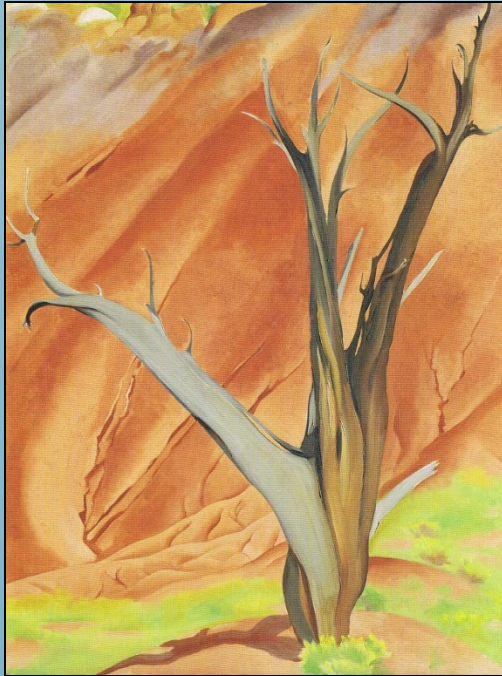


Los Alamos, 2013 (C. Allen)



Sequoia Nat. Park, 2015 (A. Das)

## ACKNOWLEDGMENTS



Dead juniper and piñon  
Georgia O'Keefe  
New Mexico 1930's



- WSL
- *Slovenia Forestry Institute*
- *Los Alamos HS students*
- *UNM Biology Dept.*
- DOE-BER
- LDRD
- IGPP
- NSF
- USDA
- USGS