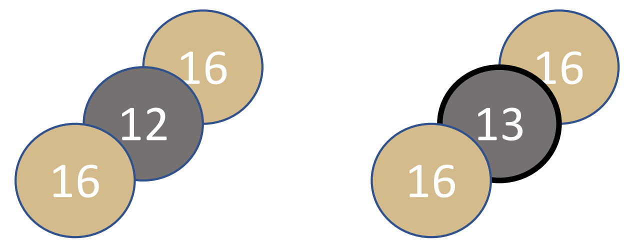
Using stable carbon isotopes to constrain terrestrial biosphere water use efficiency.

$^{12}C^{16}O_2$ $^{13}C^{16}O_2$



~400 ppm ~4 ppm

Dr. LISA WELP
Earth, Atmospheric, and Planetary Sciences
Purdue University
Twitter @WelpLisa

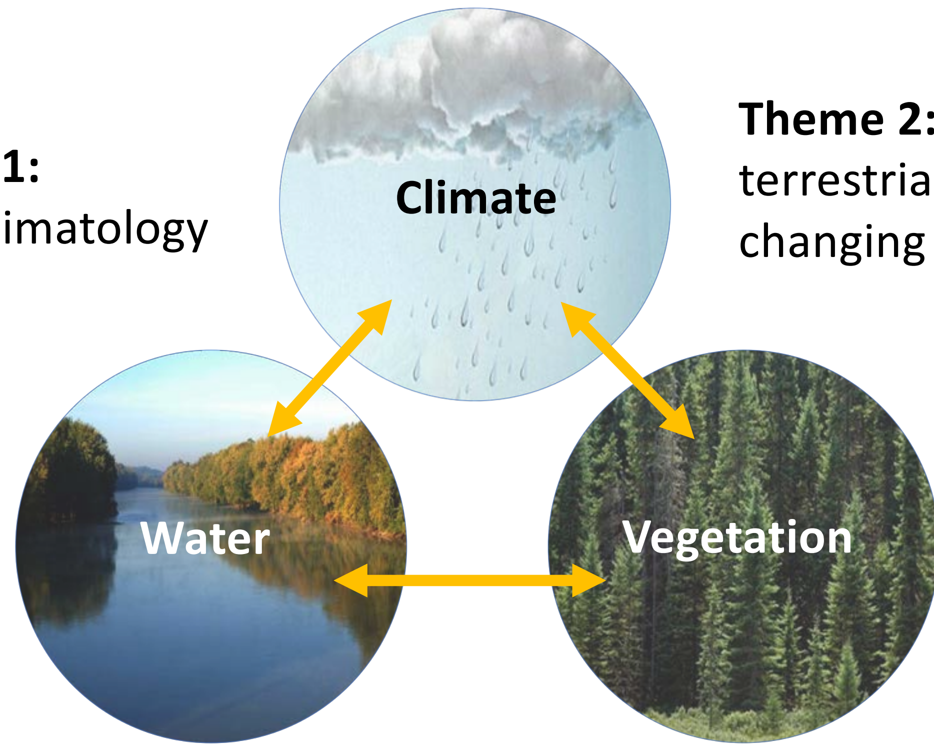
PURDUE UNIVERSITY

E^{3}SM Coupled Biogeochemistry Group Webinar
May 26, 2020

My interdisciplinary research centers on vegetation-water-climate interactions.

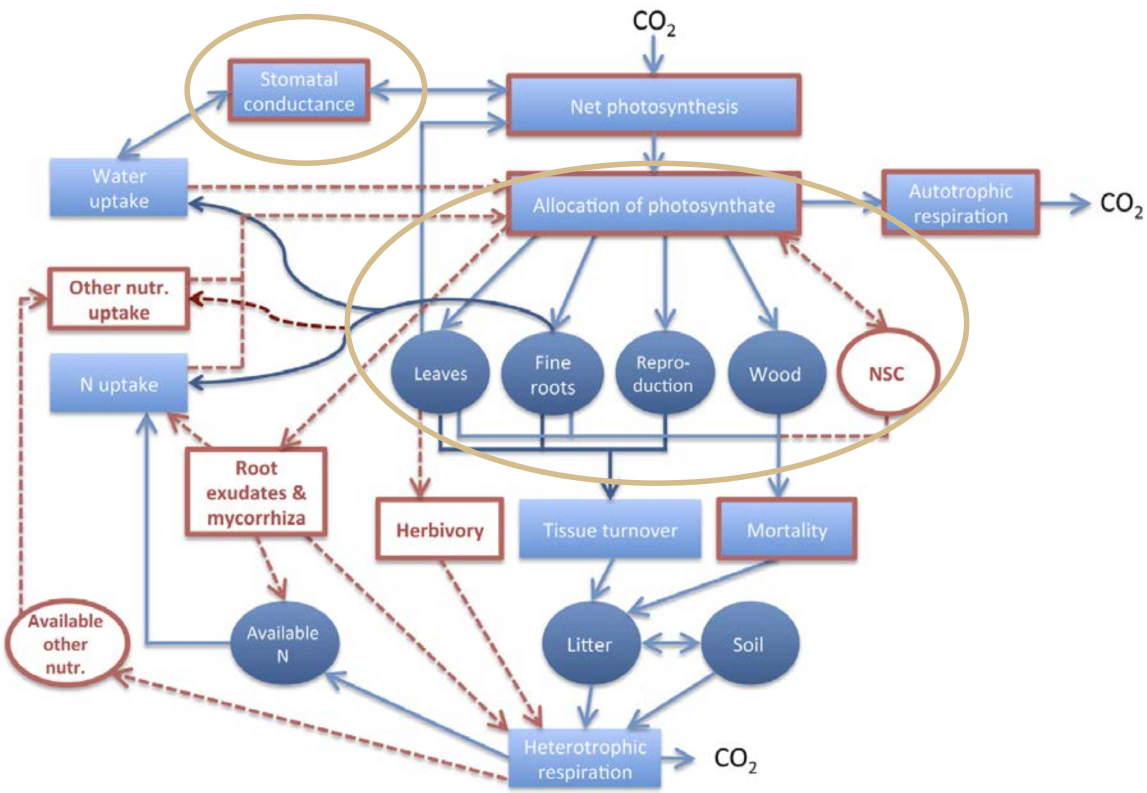
Theme 1: Hydroclimatology

Theme 2: Sensitivity of the terrestrial carbon cycle in a changing climate



Theme 3: Plant water use efficiency

Key knowledge and data gaps remain for modeling the influence of CO_2 on the terrestrial carbon sink.



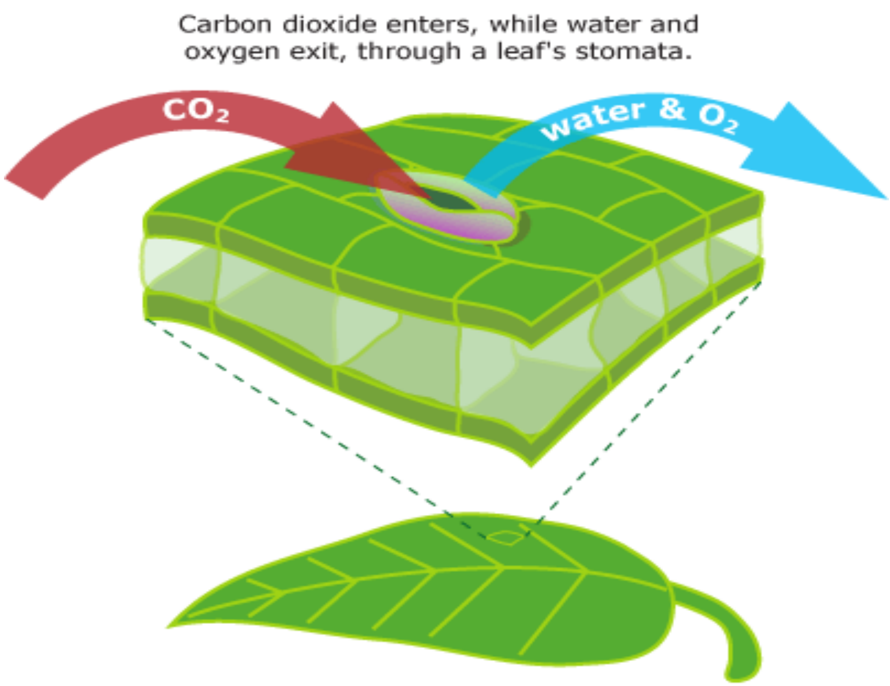
Today I'll discuss 2 of these in the context of carbon isotopes:

1) Stomatal conductance

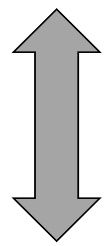
2) Allocation of photosynthesis

Pugh et al., Journal of Plant Physiology, 203, 3–15, doi:10.1016/j.jplph.2016.05.001, 2016.

Leaf stomata regulate CO_2, H_2O, and heat exchange with the atmosphere.



Energy balance



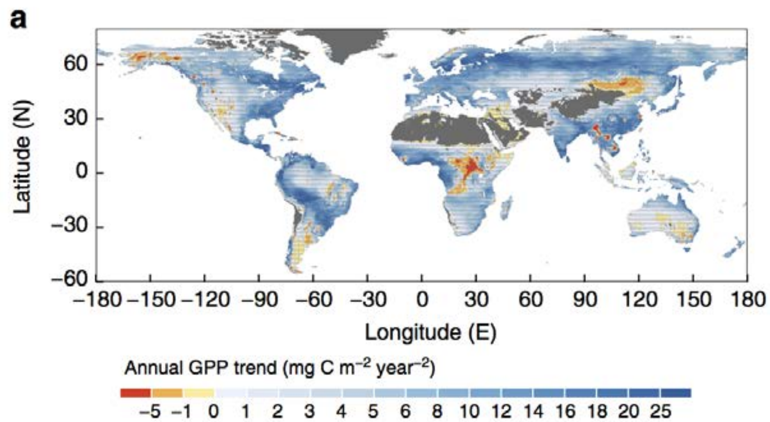
Respond to light intensity, drought stress (evaporative demand and soil moisture), atmospheric CO_2 concentrations, nutrient status and species.

Very sensitive to climate change!

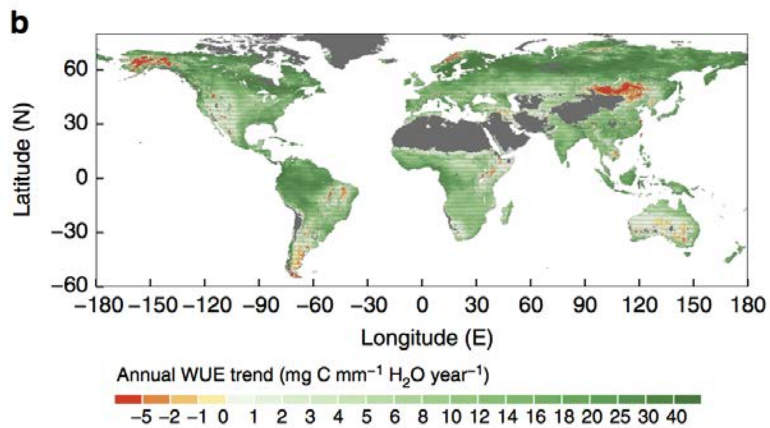
Major source of uncertainty in predicting future climate.

Berry et al. (2010) Current Opinion in Plant Biology

Photosynthesis may have increased by ~30% over the 20th century, with little extra use of water, driven by increased CO_2.



Gross Primary Production (GPP)
or net photosynthesis

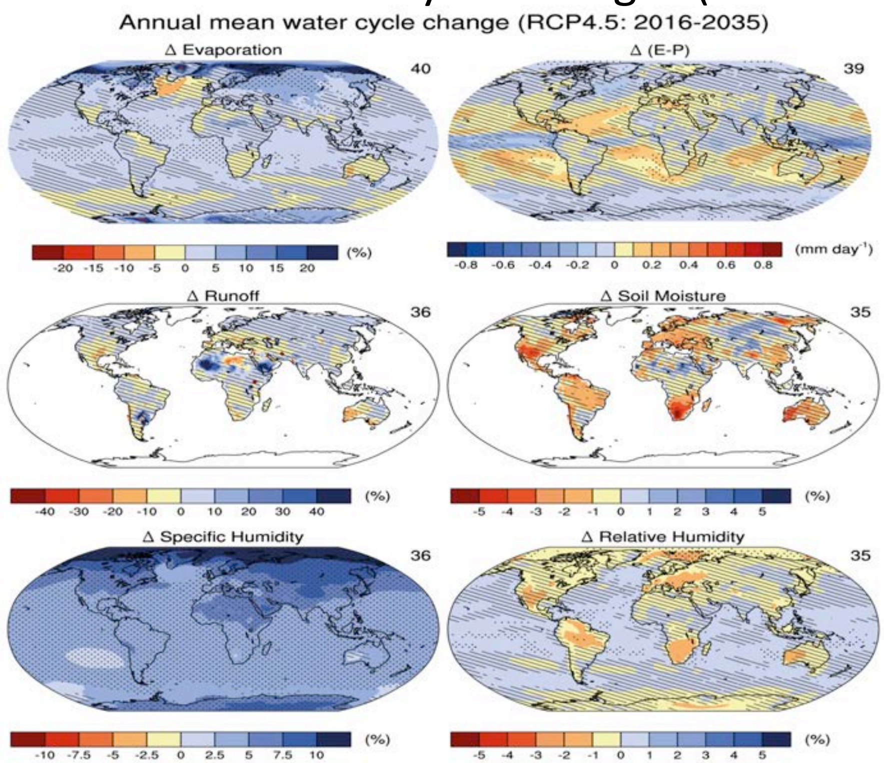


Water Use Efficiency (WUE)
= photosynthesis (g C) / transpiration (g H_2O)

Cheng et al., Nature Communications, 2017. (Figure)
Campbell et al., Nature, 544(7648), 2017. (31% increase in GPP)

Plant WUE has important consequences for the global hydrologic cycle as well as the carbon cycle.

Predicted water cycle changes (2016-2035)



IPCC AR5 Fig 11-14

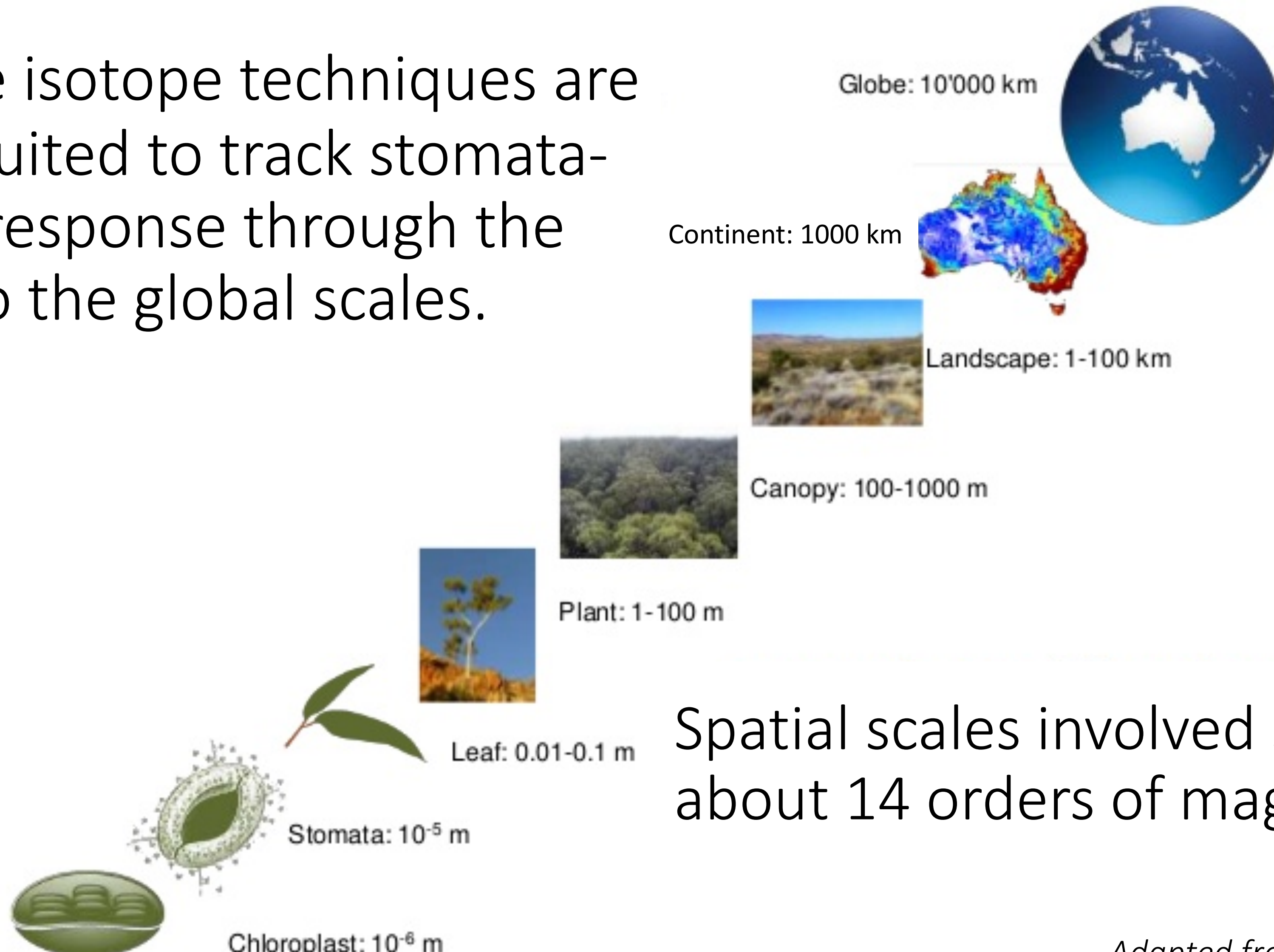
Motivating questions:

How does terrestrial ecosystem WUE change with CO_2 and drought?

How will evapotranspiration and precipitation change with climate change?

How do carbon-water feedbacks influence net carbon sinks?

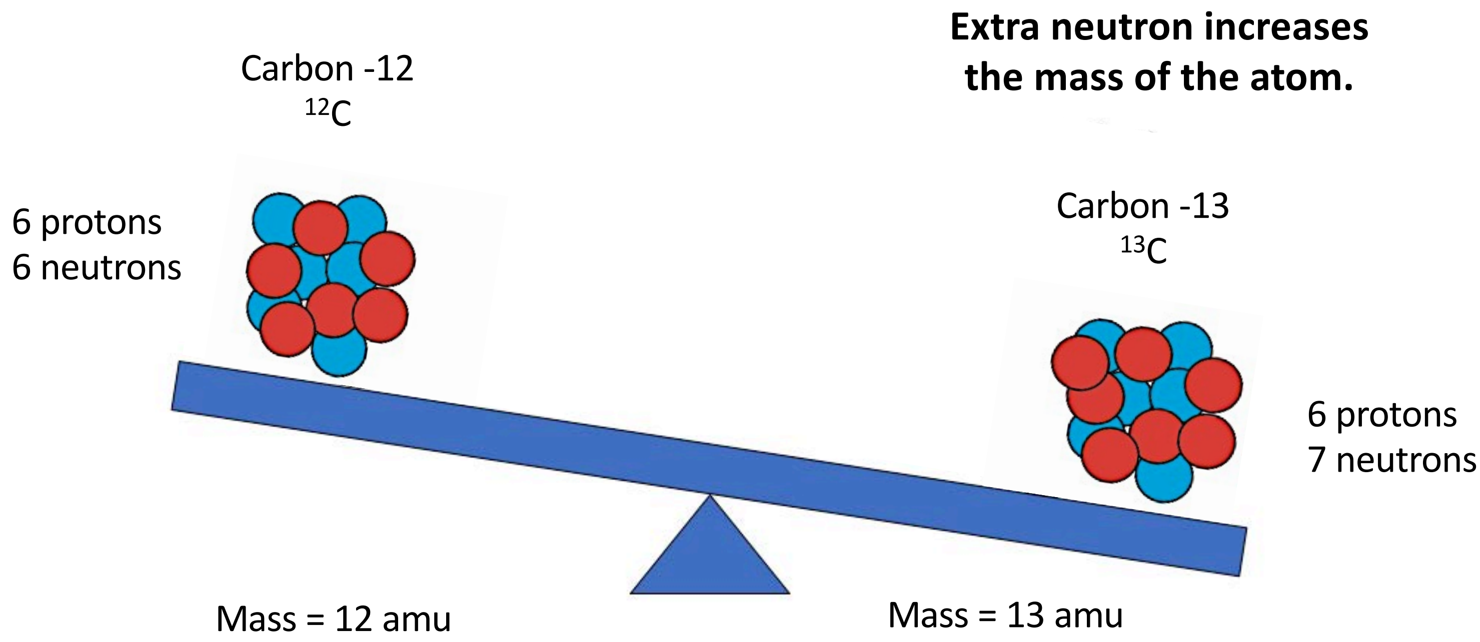
Stable isotope techniques are well suited to track stomata-level response through the leaf to the global scales.



Spatial scales involved span about 14 orders of magnitude.

Adapted from D. Baldocchi

Isotopes are the same element, but different mass because of extra neutrons.



$^{13}CO_2$ constitutes only 1.1% of the CO_2 in the atmosphere

Light isotope details

Natural abundance

^{1}H = 99.985%

^{2}H (or D) = 0.015%

^{3}H = not stable

^{12}C = 98.89 %

^{13}C = 1.11%

^{14}C = not stable

^{16}O = 99.759%

^{17}O = 0.037%

^{18}O = 0.204%

Measurement techniques

Physical separation of masses:
Isotope ratio mass spectrometry

Optical absorption of different vibrational frequencies:
New laser instruments

Delta notation

$$R = \frac{\text{heavy}}{\text{light}}$$

$$\delta = \left(\frac{R_{smp}}{R_{std}} - 1 \right) \times 1000$$

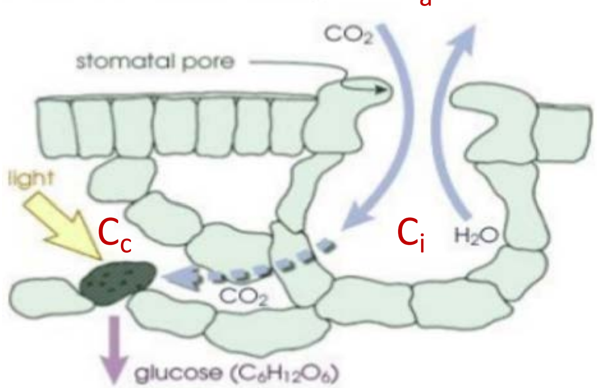
Expressed in per mil (‰)

H_2O 'types': $^{1}H_2{}^{16}O$, $^{1}H_2{}^{\mathbf{18}}\mathbf{O}$, $^{1}H^{\mathbf{2}}\mathbf{H}^{16}O$

CO_2 'types': $^{12}C^{16}O_2$, $^{\mathbf{13}}\mathbf{C}^{16}O_2$, $^{12}C^{\mathbf{18}}\mathbf{O}^{16}O$

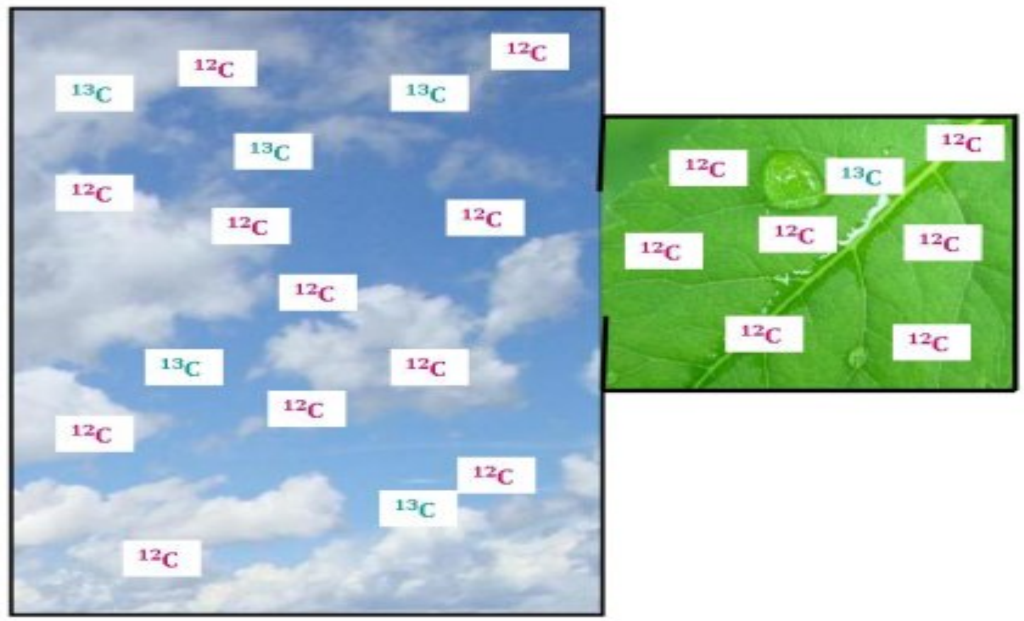
Carbon isotopes of atmospheric CO_2 and plant tissue can be used as an estimate of water use efficiency because they are sensitive to the stomatal opening size and C_i/C_a.

Lighter CO_2 diffuses into the leaf faster.



Lighter CO_2 reacts faster with Rubisco.

The atmospheric $^{13}C/^{12}C$ ratio is higher than the plant $^{13}C/^{12}C$ ratio



Photosynthesis favors $^{12}CO_2$ over $^{13}CO_2$ and the magnitude of the difference depends on C_i/C_a.

Photosynthetic ^{13}C discrimination ($\Delta^{13}C$) in C_3 plants depends on:

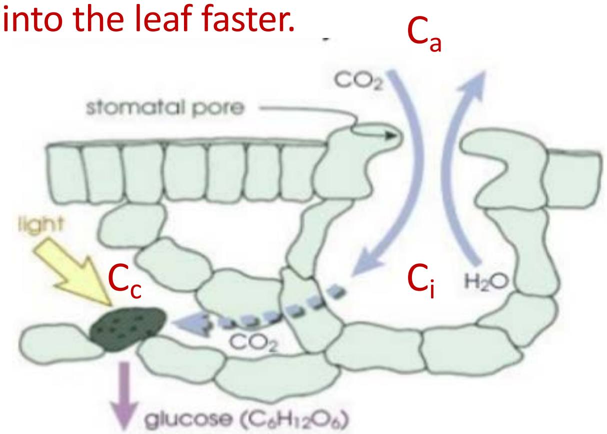
$$\Delta^{13}C \approx \delta_{plant} - \delta_{atm} \approx a + (b' - a)\frac{C_i}{C_a}$$

Diffusion of CO_2 through air

Enzyme fractionation against ^{13}C

Ratio of intercellular CO_2 to atmospheric CO_2 concentration

Lighter CO_2 diffuses into the leaf faster.



Lighter CO_2 reacts faster with Rubisco.

Farquhar et al., 1989

δ^{13}C measurements of plant tissue and the atmosphere can be used to estimate intrinsic water use efficiency.

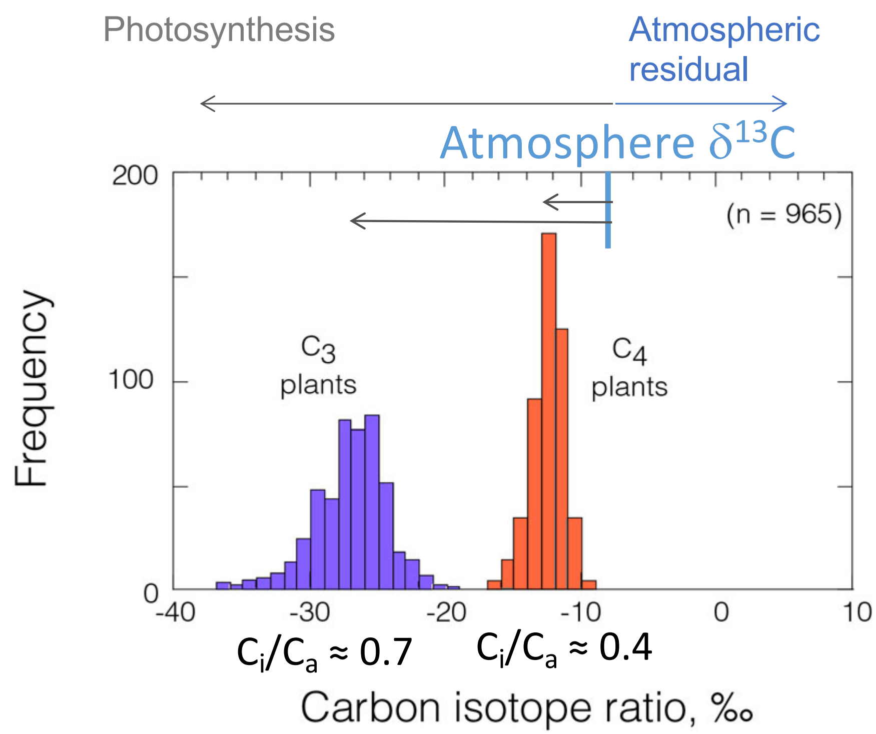
$$\Delta^{13}C \approx \delta_{plant} - \delta_{atm} \approx a + (b' - a)\frac{C_i}{C_a}$$

Intrinsic water use efficiency (iWUE) can be calculated from C_i/C_a:

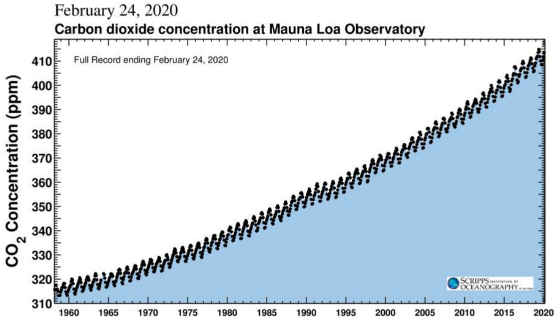
i*WUE* = $A/g_{s,H2O}$ = $C_a(1 - C_i/C_a)/1.6$

Physiological response of WUE or the part that is not controlled by VPD demand.

$A = 1.6 * g_{s,H2O}(C_a - C_i)$



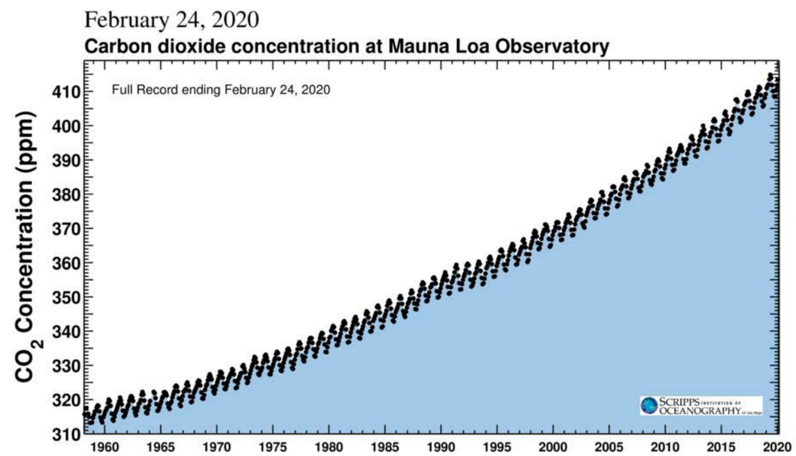
Two stories today:
Examples from atmospheric residuals and plant tissues



Atmospheric investigation: Trends in stomata conductance due to increased atmospheric CO_2 concentrations. Long-term global and regional changes in terrestrial ecosystem intrinsic WUE from the atmospheric $\delta^{13}C$ of CO_2 record.

Plant tissue investigation: Role of carbon allocation in interpreting plant tissue $\delta^{13}C$. Seasonal and intra-annual variability in ^{13}C of plant tissues.

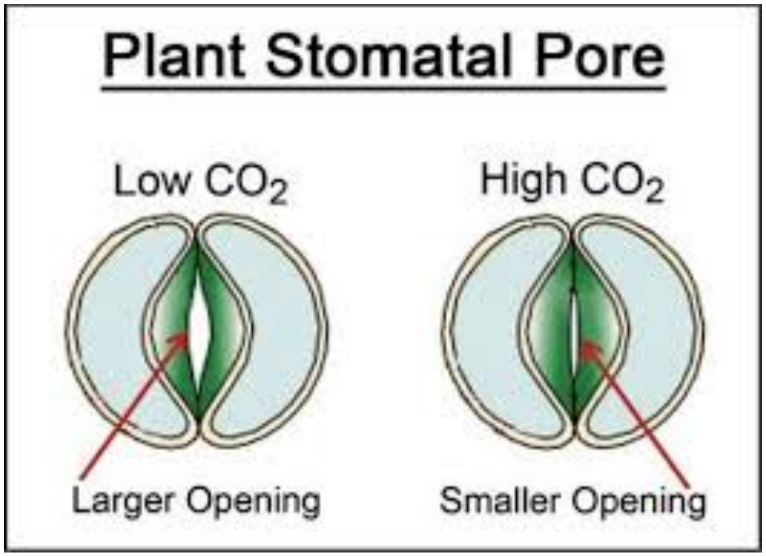
Global scale, response to CO_2



How has the terrestrial biosphere responded to increasing atmospheric CO_2 and climate change over the past few decades?

Keeling, R.F., H.D. Graven, L.R. Welp, L. Resplandy, J. Bi, S.C. Piper, Y. Sun, A. Bollenbacher, and H.A.J. Meijer (2017) **Atmospheric evidence for a global secular increase in carbon isotopic discrimination of land photosynthesis**, *Proceedings of the National Academy of Sciences*, 114(39), 10361-10366, doi:10.1073/pnas.1619240114.

Stomatal aperture is sensitive to atmospheric CO_2 concentration.

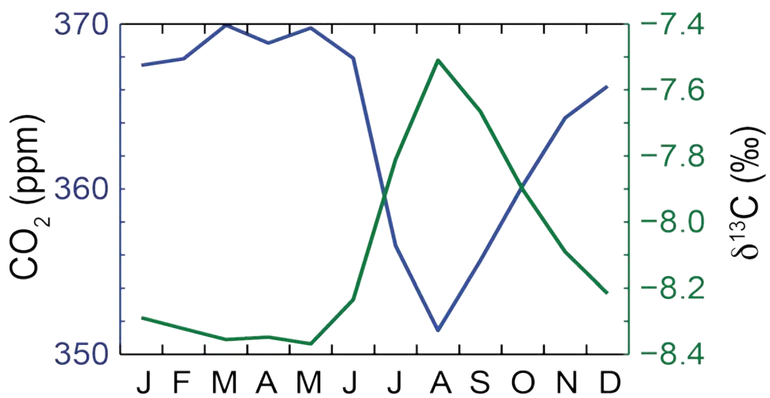


Reducing the size of leaf stomata may be advantageous for a plant in a water limited environment.

It can still get enough CO_2 while conserving water loss, thereby improving intrinsic water use efficiency.

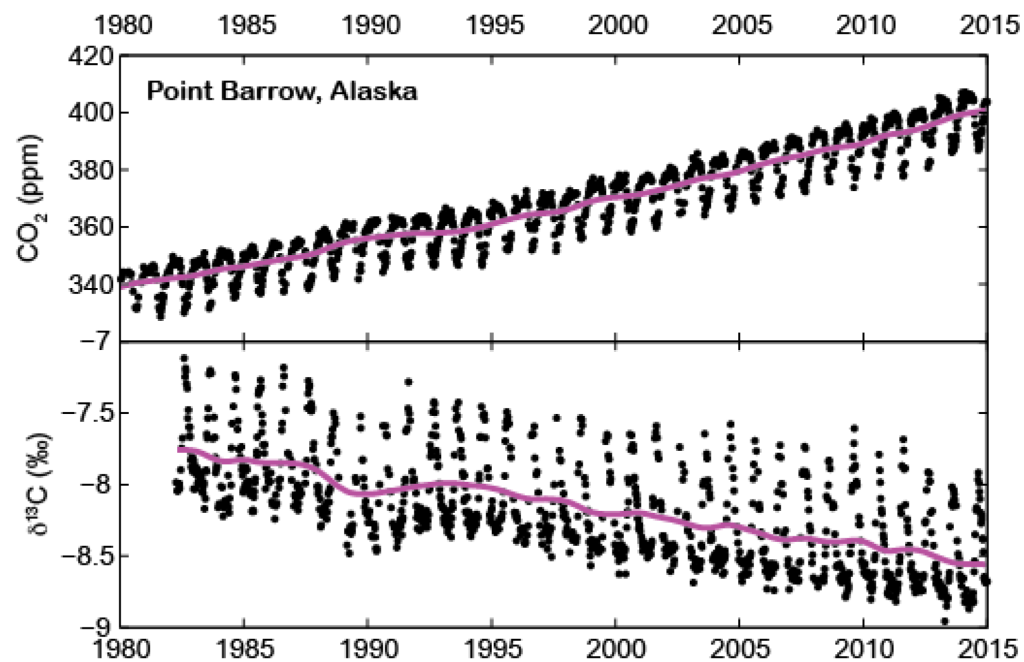
However, temperature stress may increase.

When plants remove CO_2 from the atmosphere, the $\delta^{13}C$ of the residual air increases, sensitive to average plant iWUE.



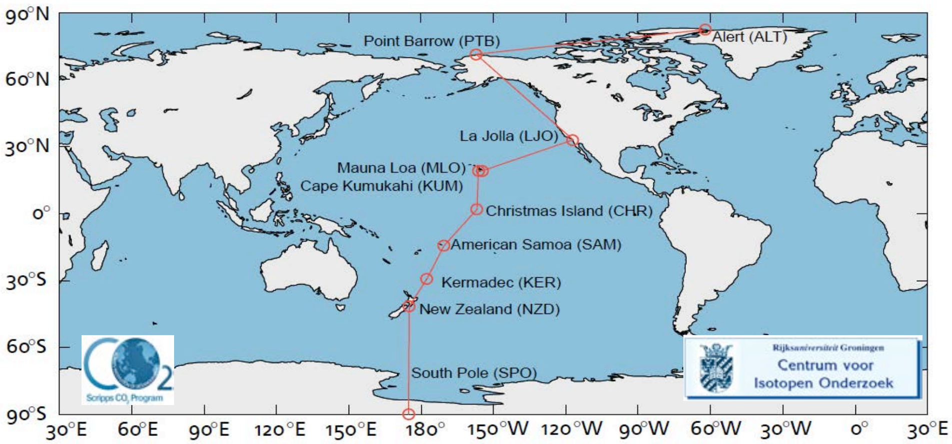
When CO_2 decreases in the summer, $\delta^{13}C$ increases.

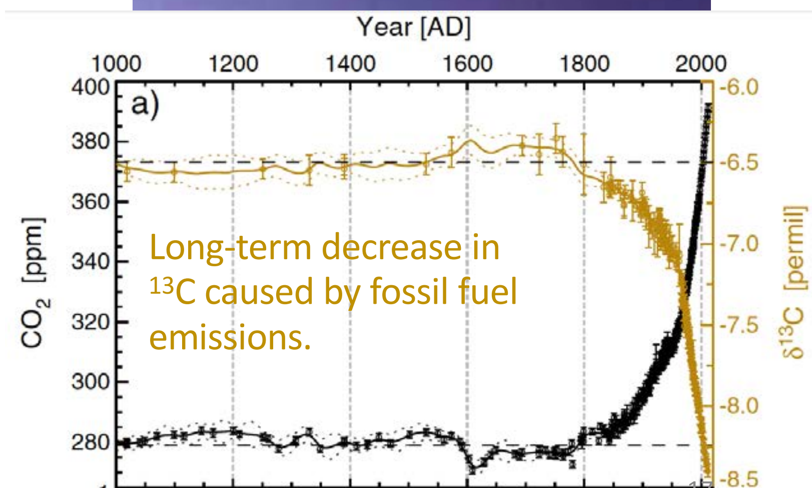
The atmospheric $\delta^{13}C$ is the inverse of the signal in plant tissues.



Seasonality is dominated by the biosphere activity.
Long-term trends are dominated by fossil fuel emissions.

Long term records of atmospheric CO_2 $\delta^{13}C$ change from the Scripps CO_2 flask network since 1978 and ice core records before that.



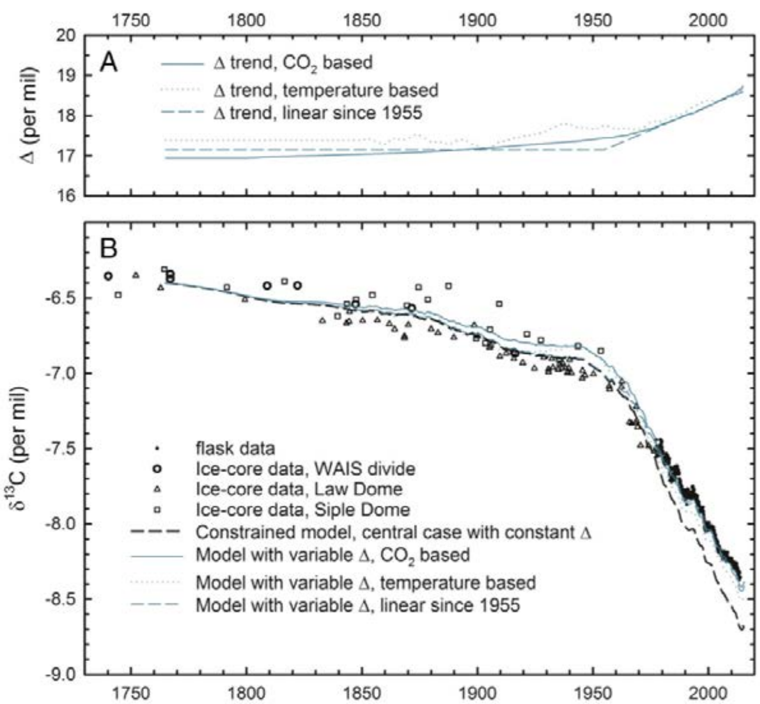


Francey et al., 1999; updated Rubino et al., 2013

Two ways to interpret the $\delta^{13}C$ of CO_2 record

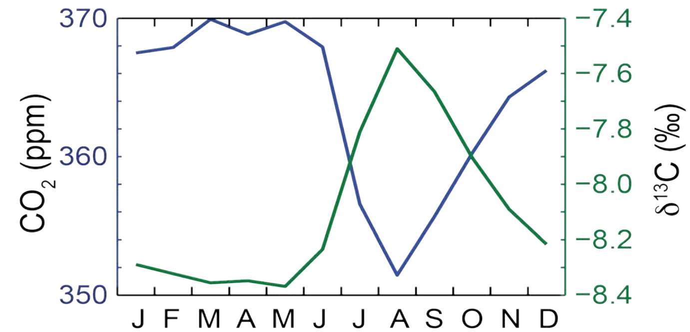
Long-term trend

(Keeling et al., 2017)



Annual seasonal cycle

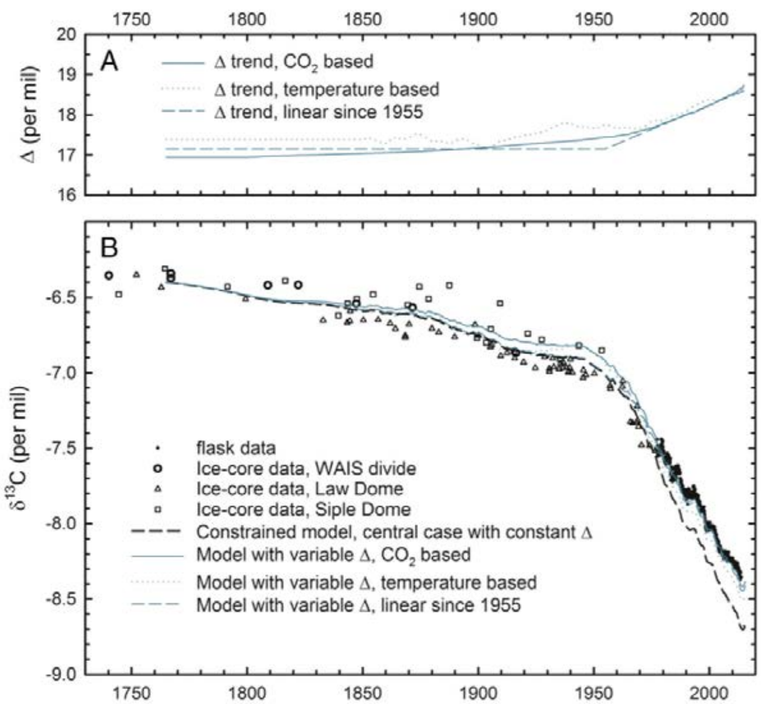
(in preparation)



When CO_2 decreases in the summer, $\delta^{13}C$ increases.

Keeling et al., Atmospheric evidence for a global secular increase in carbon isotopic discrimination of land photosynthesis, P. Natl. Acad. Sci. USA, 8, 201619240, doi:10.3402/tellusb.v39i1-2.15325, 2017.

By matching the observed $\delta^{13}C$ curve to models assuming no or variable ^{13}C discrimination with time, we can tell how plant iWUE changed.



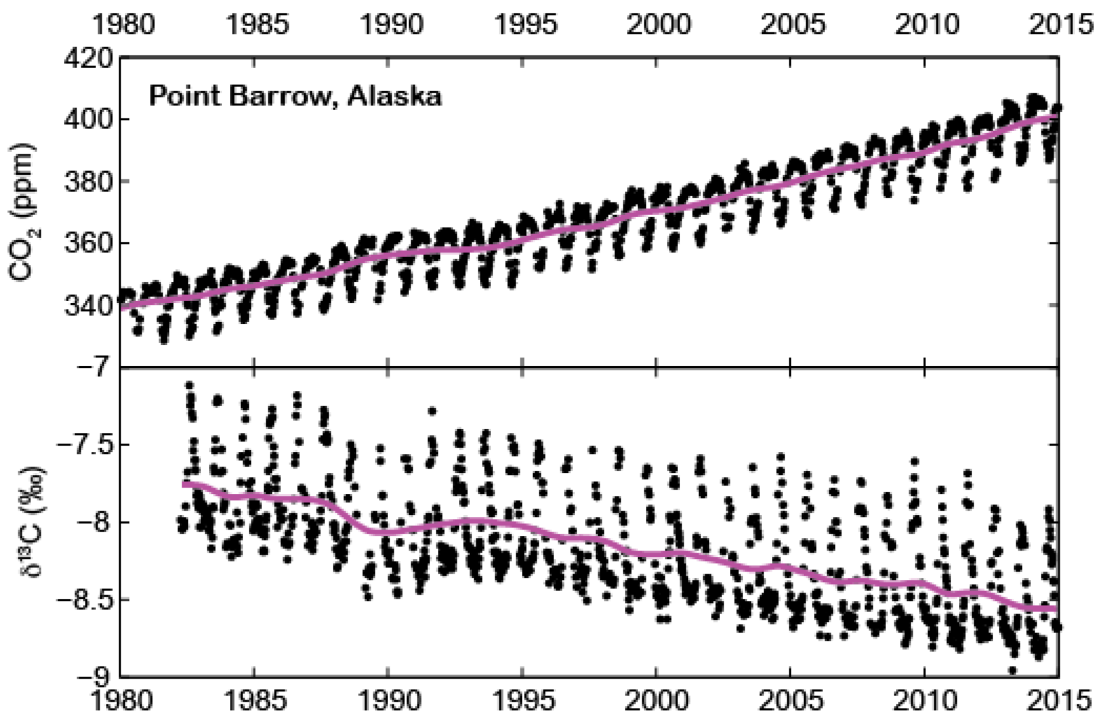
The better fit to observations by the blue curves show that some increase in $\Delta^{13}C$ discrimination has occurred over this time.

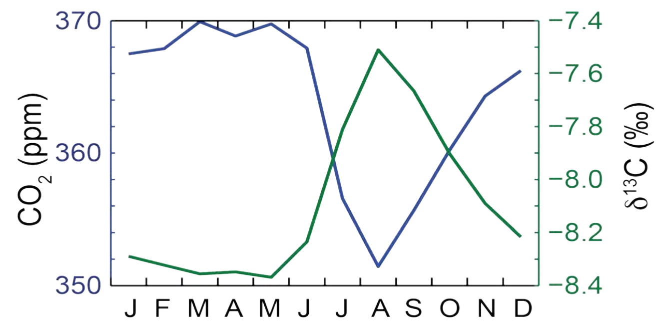
Changes in $\Delta^{13}C$ can be related to changes in C_i/C_a if the influence of mesophyll conductance and photorespiration is removed, which in turn constrains the stomatal conductance and iWUE influencing both CO_2 gain and water loss.

$$\Delta = a + (b-a)(C_i/C_a) - (b-a_m)(A/C_a)/g_i - f\Gamma^*/C_a$$

$$\mathrm{iWUE} = A/g_s = C_a(1 - C_i/C_a)/1.6$$

Using the seasonal co-variation of CO_2 and $\delta^{13}C$ to calculate the ^{13}C discrimination of the terrestrial biosphere.



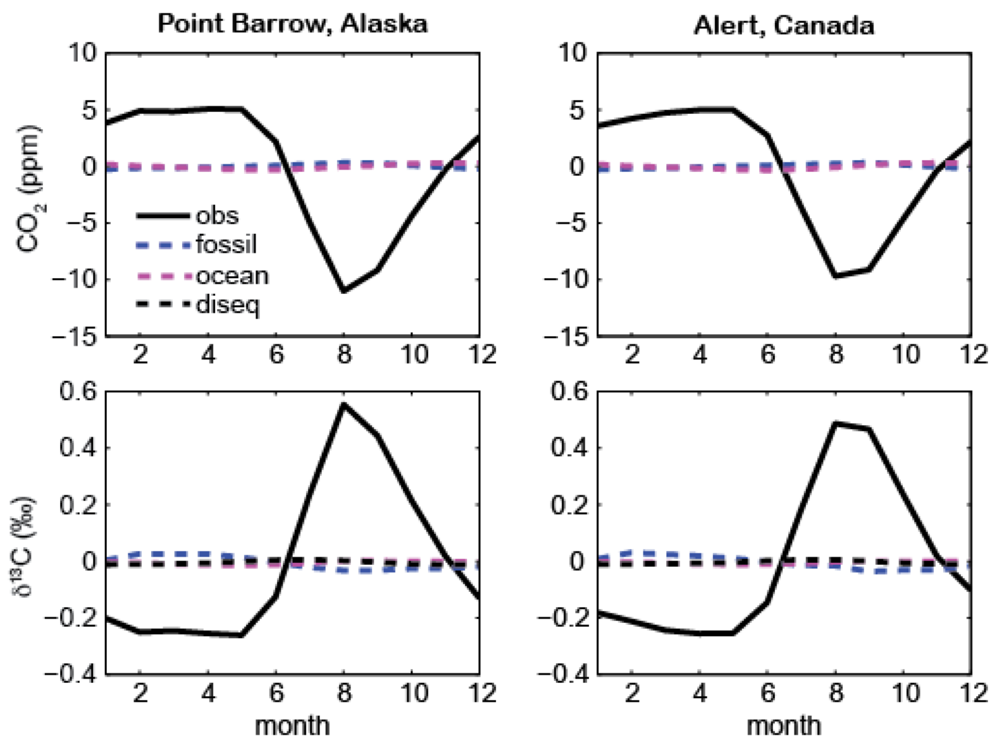


When CO_2 decreases in the summer, $\delta^{13}C$ increases.

Seasonality is dominated by the biosphere activity.
Long-term trends are dominated by fossil fuel emissions.

Because of the trends, first we subtract a 'background'

Seasonality of CO_2 and $\delta^{13}C$ is dominated by the terrestrial biosphere activity.

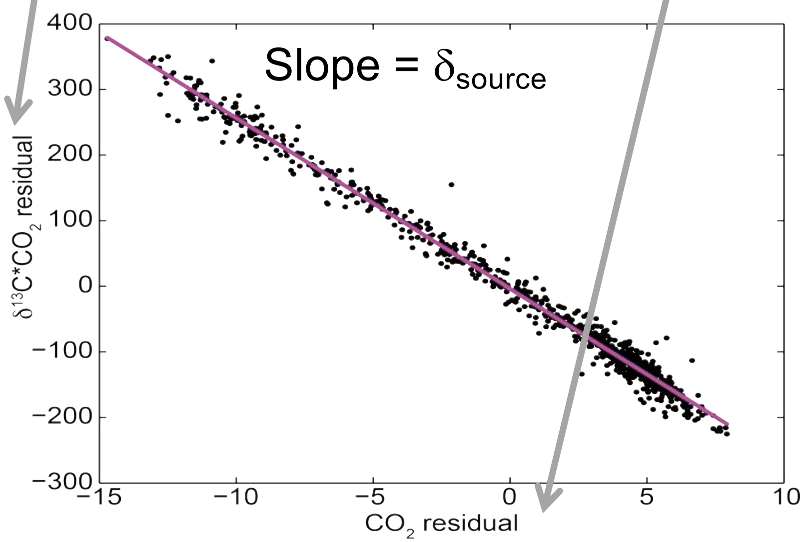


Fossil fuel emissions from CDIAC, CCSM ocean fluxes, and CASA isotopic disequilibrium fluxes were transported in TM3 and sampled at the observing location.

They have almost no effect on CO_2 or $\delta^{13}C$ seasonality, but they do become important when quantifying small trends in $\Delta^{13}C$.

Calculate $\delta^{13}C$ of photosynthetic uptake (δ_{source}) and apparent ^{13}C discrimination by the biosphere (Δ_{ap})

$$\delta_{obs}C_{obs} - \delta_{bk}C_{bk} = \delta_{source}(C_{obs} - C_{bk})$$



Apparent ^{13}C discrimination

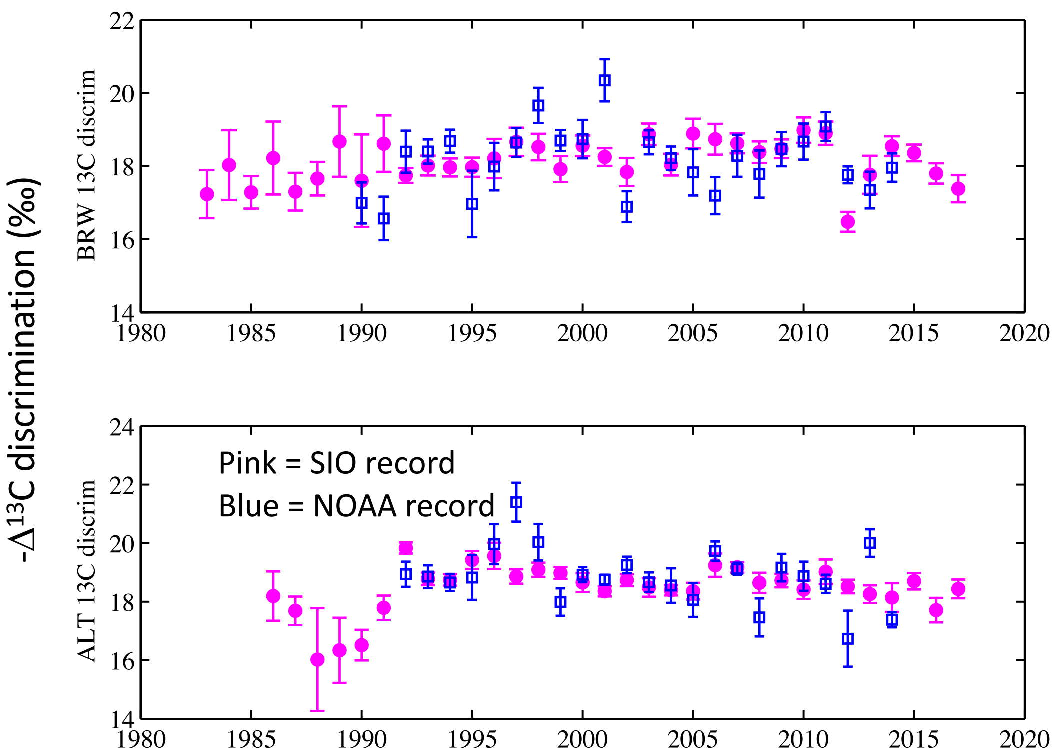
$$\Delta_{ap} = \frac{\delta_{source} - \delta_{bk}}{1 + \delta_{bk}}$$

Approximates the Land ^{13}C discrimination

$$\Delta_{al} = a + (b' - a)\frac{C_i}{C_a}$$

Miller and Tans (2003) approach

Calculate the slope fit for each year to determine how ^{13}C discrimination changes over time.



Compare calculations using SIO data to independent NOAA ESRL data.

Mean $\Delta_{apparent}$ of ~ 19‰ is consistent with dominant C_3 photosynthetic pathway.

Year-to-year variability may be caused by regional droughts or differences in air mass influences and different data screening approaches.

Trend at BRW = +0.17 ± 0.27 ‰ $decade^{-1}$.

To attribute trends to C_3 ecosystem changes, corrections are needed for fossil fuel emission influence, ocean gas exchange, isotopic disequilibrium, and maize (C_4) production.

$$d\Delta/dt = d\Delta_{apparent}/dt + corr_{fossil\ fuel} + corr_{ocean} + corr_{maize}$$

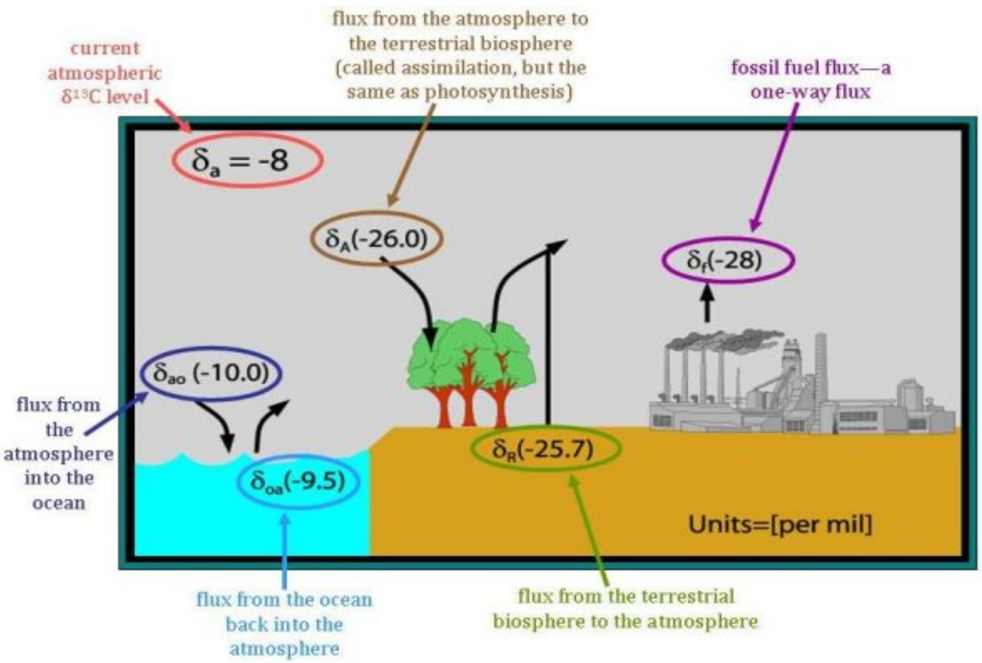


Image: http://www.esrl.noaa.gov/gmd/outreach/isotopes/c13tellsus.html

Units: ‰ decade^{-1}

$d\Delta_{apparent}/dt$	=	$+0.17 \pm 0.27$
$corr_{ocean}$	=	-0.12 ± 0.06
$corr_{fossil\ fuel}$	=	$+0.03 \pm 0.20$
$corr_{maize}$	=	$+0.17 \pm 0.08$

Actual change in C_3 discrimination for high latitudes:

$d\Delta/dt$ (1985-2017) = 0.25 ± 0.35

Both atmospheric $\delta^{13}C$ methods point to increasing ^{13}C discrimination.

Seasonal cycle (1985-2017)

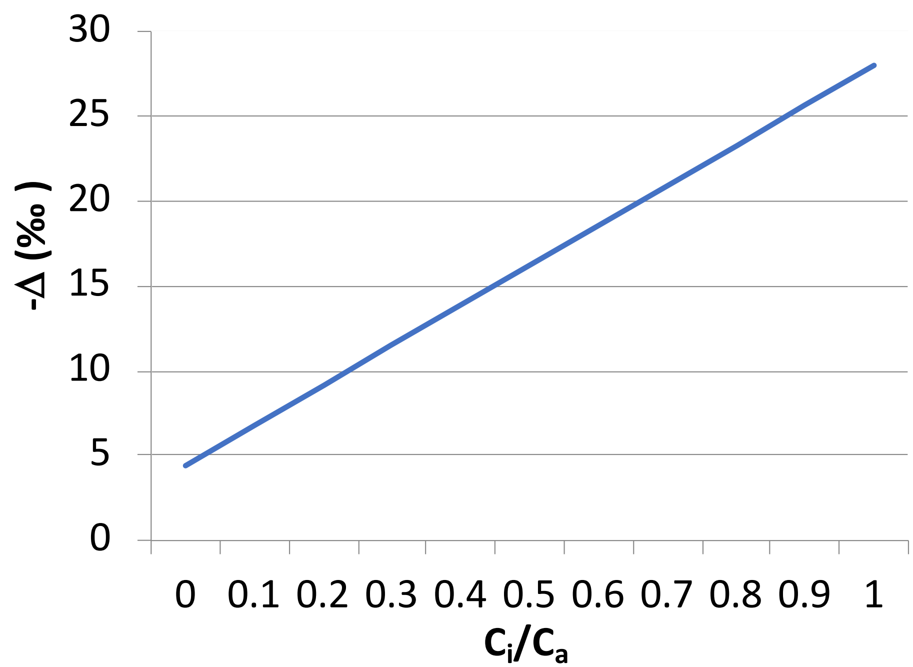
Sensitive to temperate to Arctic

0.25 ± 0.35‰ decade^{-1}

Long-term trend (1975-2005)

Sensitive to the tropics

0.22 ± 0.11‰ decade^{-1}

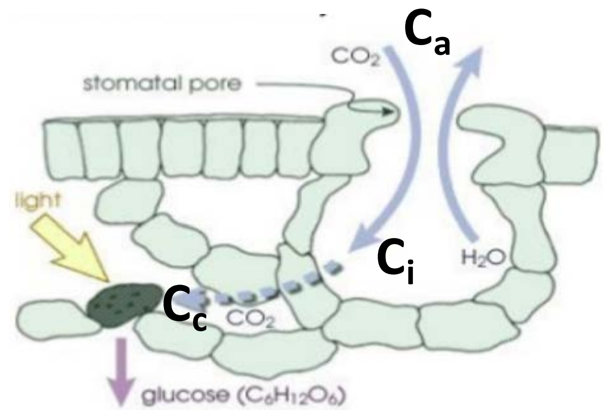


What does this mean for C_i/C_a and iWUE trends?

Convert ^{13}C discrimination to C_i/C_a and iWUE

Linear approximation:

$$\Delta = a + (b' - a)\frac{C_i}{C_a}$$



More precise version:

Eqns from Seibt et al. 2008

$$\Delta = a + (b - a)\frac{C_i}{C_a} - (b - a_m)\frac{A}{g_m C_a} - f\frac{\Gamma_*}{C_a}$$

Mesophyll conductance term

Photorespiration term

Solve for C_i/C_a…

Intrinsic WUE $= A/g_s$

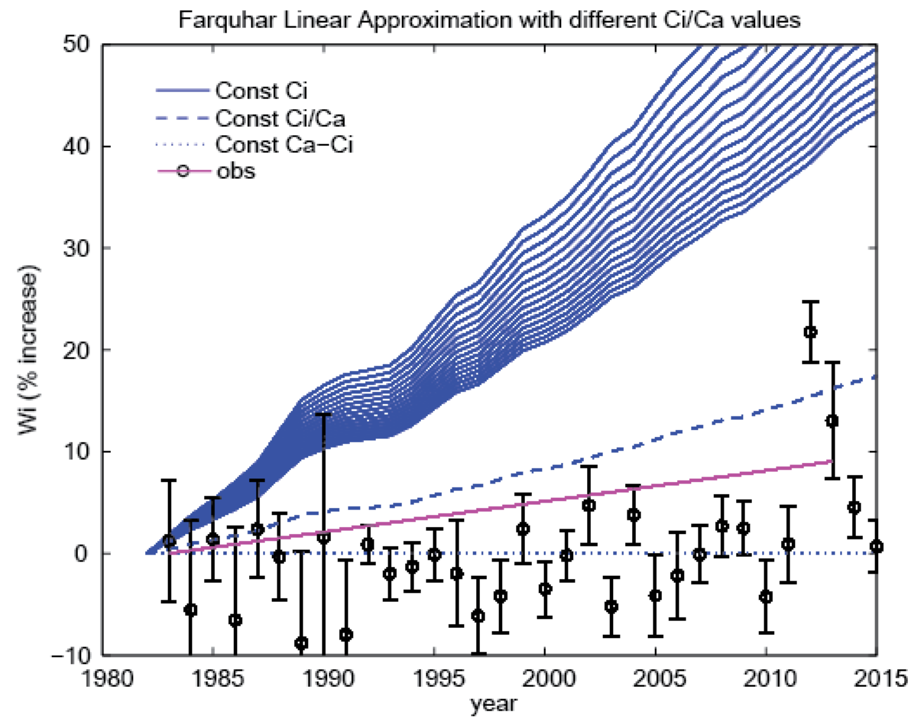
$= C_a(1 - C_i/C_a)/1.6$

C_a increased by ~55 ppm from 1985 to 2017.

The mesophyll and photorespiration terms contribute 0.010 ± 0.004‰ ppm^{-1}.

C_i/C_a trend ~constant and increase in iWUE as atmospheric CO_2 increased.

Intrinsic WUE $= C_a(1 - C_i/C_a)/1.6$



Seasonal cycle (1985-2017)

Sensitive to temperate to Arctic

iWUE increased 14 ± 18%

CO_2 rose by 18%

Long-term trend (1975-2005)

Sensitive to the tropics

iWUE increased by 11 ± 6%

CO_2 rose by 14%

Ecosystems from the tropics to the temperate mid-latitudes and the Arctic are all increasing iWUE with increased atmospheric CO_2.

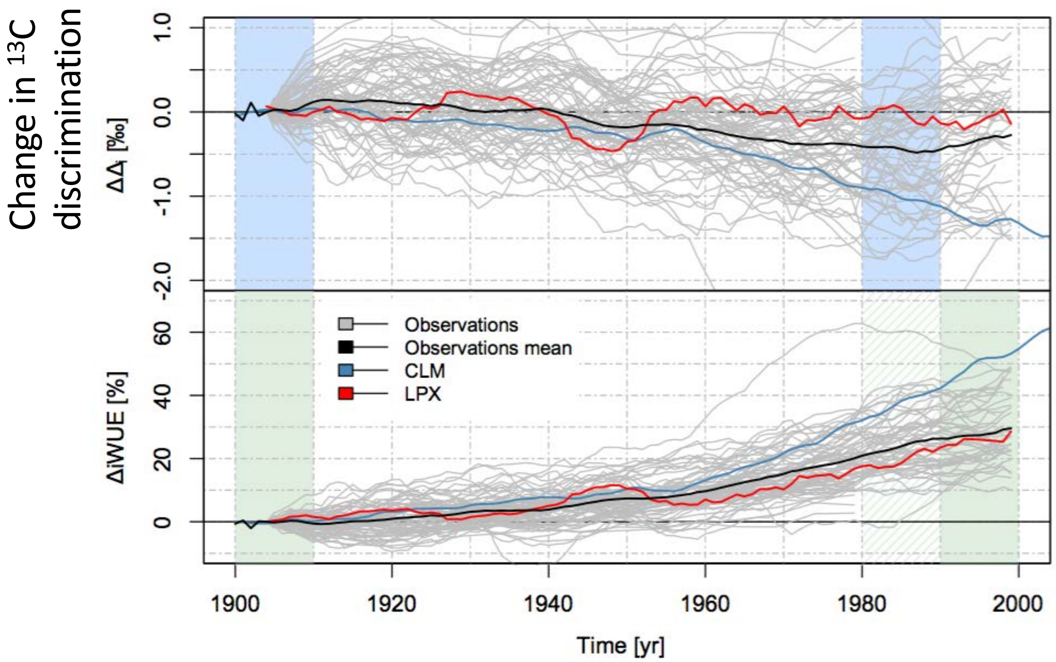
The atmospheric results imply constant C_i/C_a values and a 20% increase in iWUE over the 20th century in response to increasing CO_2, consistent with trends in tree-ring records.

$$\Delta = a + (b-a)(C_i/C_a) - (b-a_m)(A/C_a)/g_i - f\Gamma^*/C_a$$

$$\mathrm{iWUE} = A/g_s = C_a(1 - C_i/C_a)/1.6$$

- Photosynthetic ^{13}C discrimination can be measured on individual tree rings to reconstruct changes over time.
- Recent efforts using northern hemisphere tree species also observe ^{13}C trends consistent with constant C_i/C_a (Frank et al., 2015 , Keller et al, 2017).
- Consistent with stomatal optimization theory which predicts a constant C_i/C_a and a 1% increase in C_a will result in a 1% increase in iWUE (Medlyn et al., 2011). Assumes that plants adjust their stomatal conductance to maximize overall carbon gain, also considering the metabolic costs of supplying water for transpiration.

As more carbon cycle models incorporate ^{13}C, these records provide important validation.

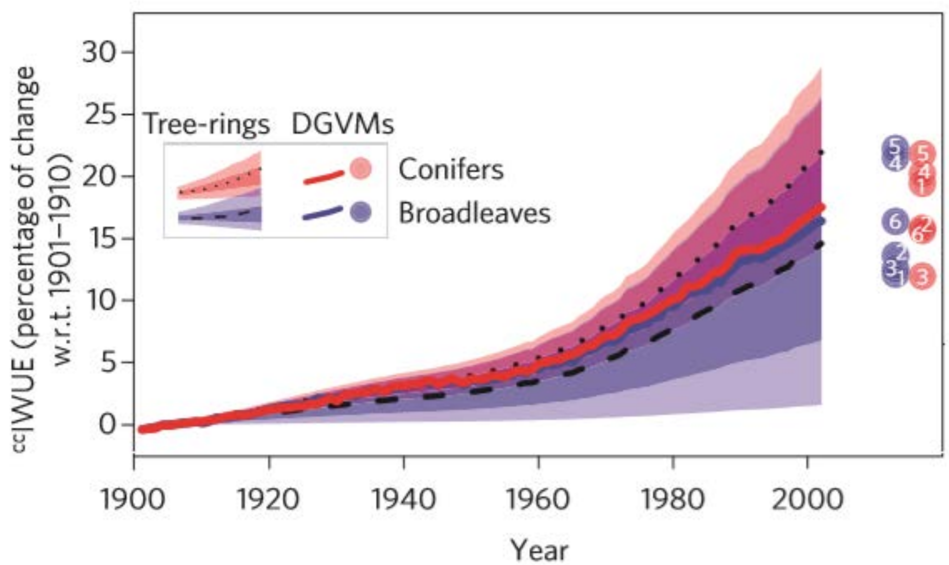


LPX matches tree-ring ^{13}C records more closely than CLM.

Tree ring records and atmospheric observations are converging on constant C_i/C_a trends as C_a increases.

Keller et al., 20th century changes in carbon isotopes and water-use efficiency: tree-ring-based evaluation of the CLM4.5 and LPX-Bern models, Biogeosciences, 14(10), 2641–2673, doi:10.1002/eap.1490, 2017.

While overall patterns are converging, different plant functional types and species differ in their iWUE responses.



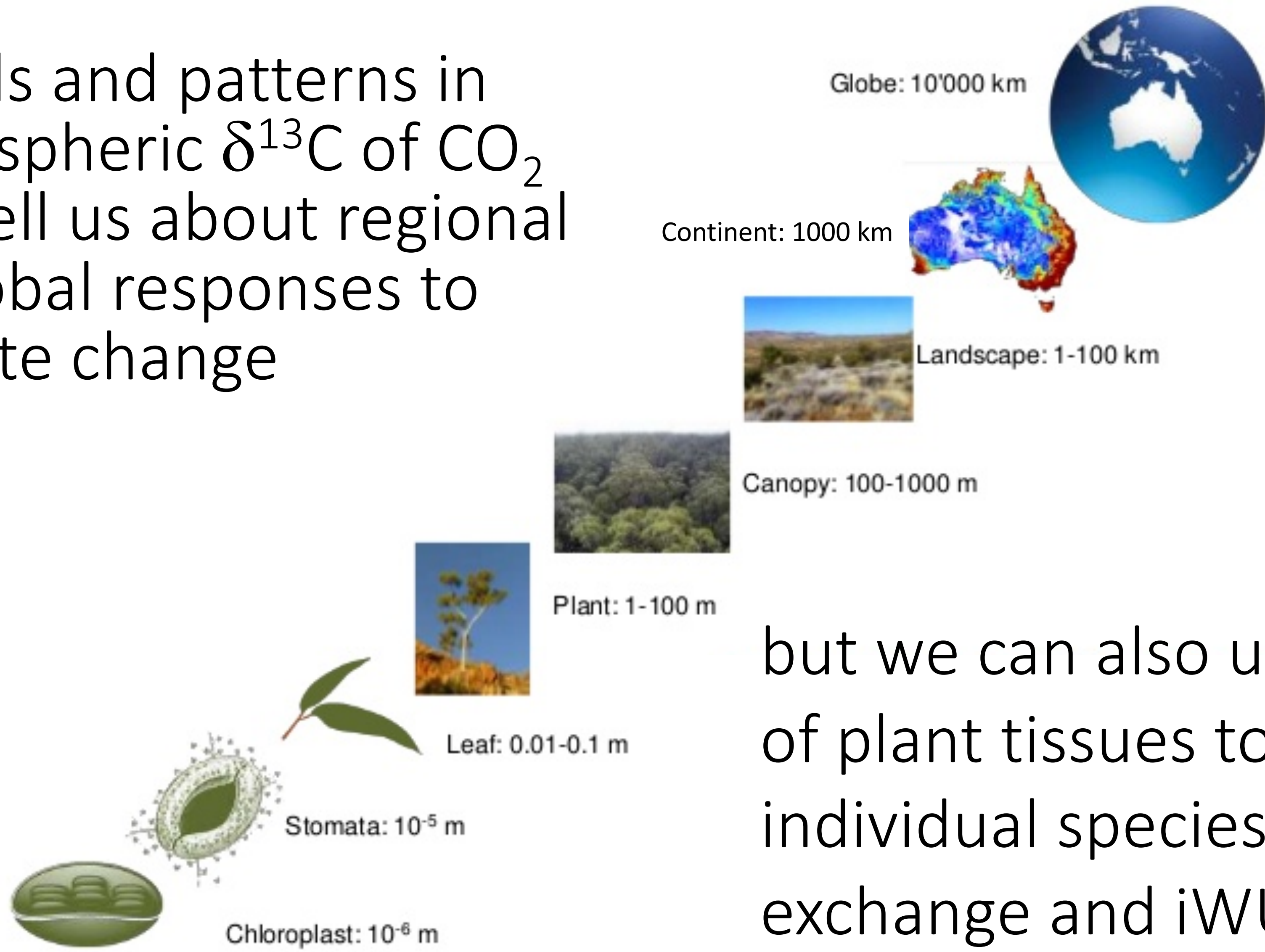
For example, conifer and broadleaf trees were found to have different $\delta^{13}C$ trends and iWUE (Frank et al., 2015).

Not accounting for age and development effects may lead to erroneous conclusions (Brienen et al., 2017).

Let's consider individual tree species now…

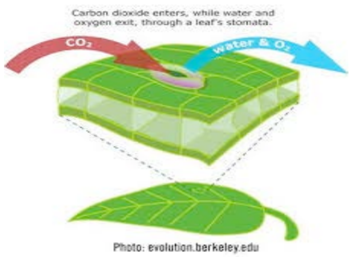
Frank et al., 2015, Nature Climate Change

Trends and patterns in atmospheric $\delta^{13}C$ of CO_2 can tell us about regional to global responses to climate change



but we can also use $\delta^{13}C$ of plant tissues to study individual species gas exchange and iWUE.

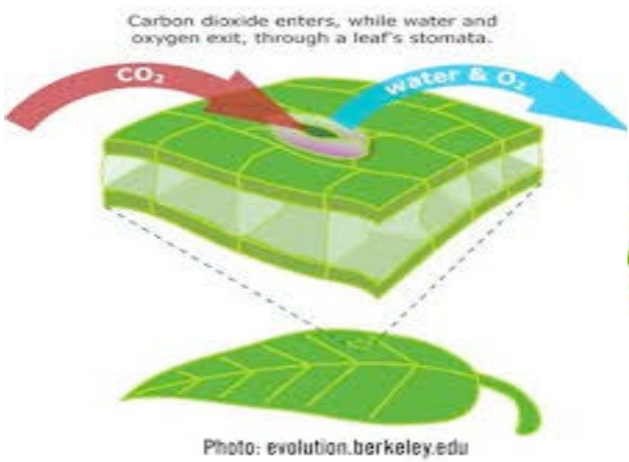
Leaf to canopy scale, Internal carbon allocation



Carbon allocation in trees influences the intrinsic WUE estimate.

Oh, Y., L.R. Welp, K. Yi, M.C. Benson, K.A. Novick, Q. Zhuang, and D. Lombardozzi (*submitting this week*) **Carbon allocation affects seasonal leaf carbon isotopic signatures and inferred water use efficiency of temperate deciduous trees**.

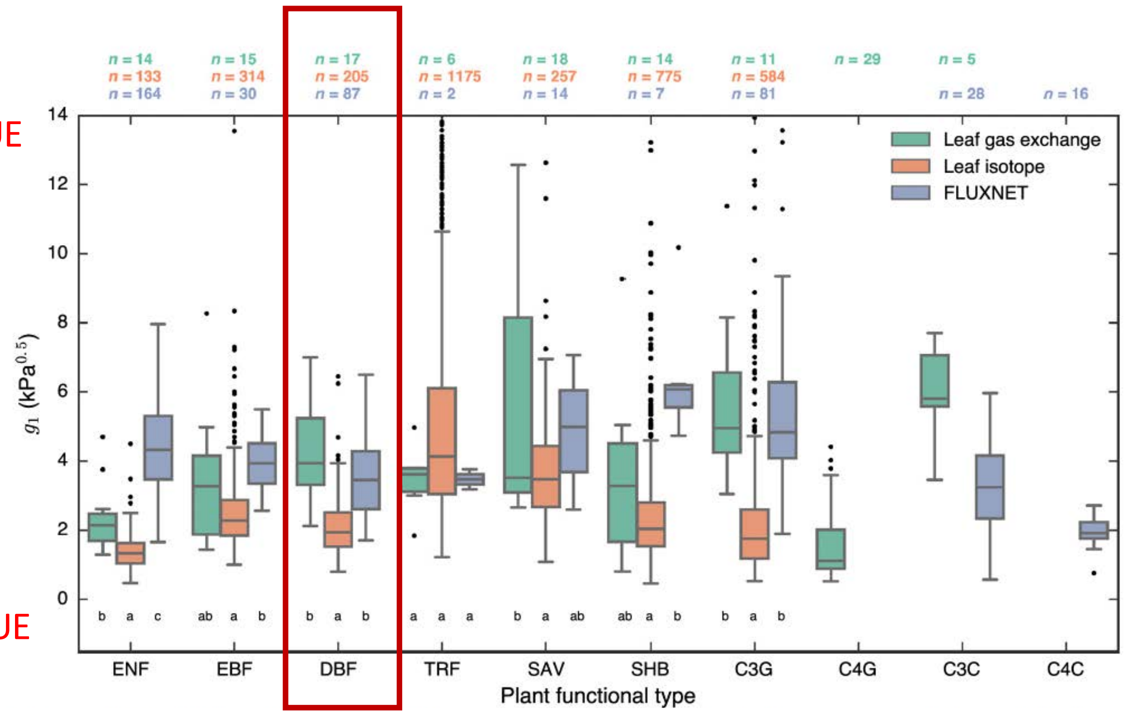
There are many different ways and scales to measure plant water use efficiency (WUE).



Spatial scale:	Leaf	Whole plant	Ecosystem or field
Temporal:	Instantaneous	Daily-to-annual	Daily-to-annual
Methods:	chamber, **$^{13}C/^{12}C$**	Sap flux sensor (non-photosynthetic water loss)	Eddy covariance (soil evaporation)

WUE can be estimated using leaf gas exchange, ^{13}C, and eddy covariance, but they give different results.

Low WUE



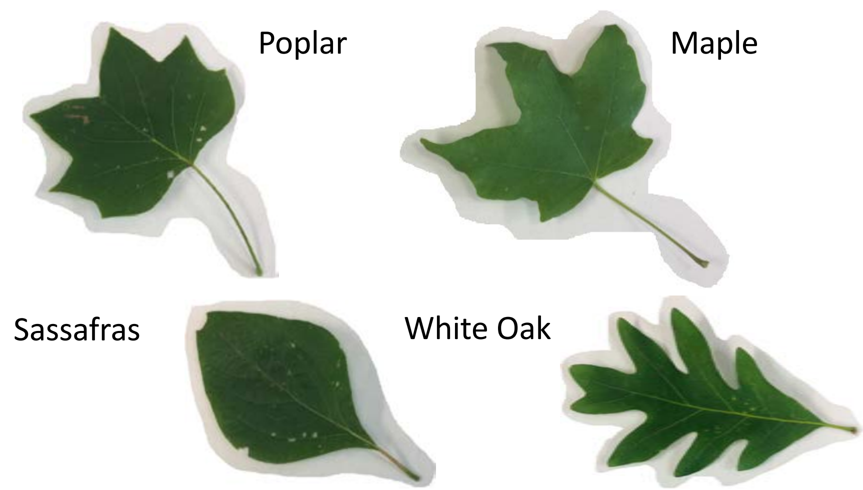
High WUE

Leaf isotope-based estimates of WUE are higher than other estimates, indicating a key research direction to reconcile measures of WUE.

Medlyn et al., 2017

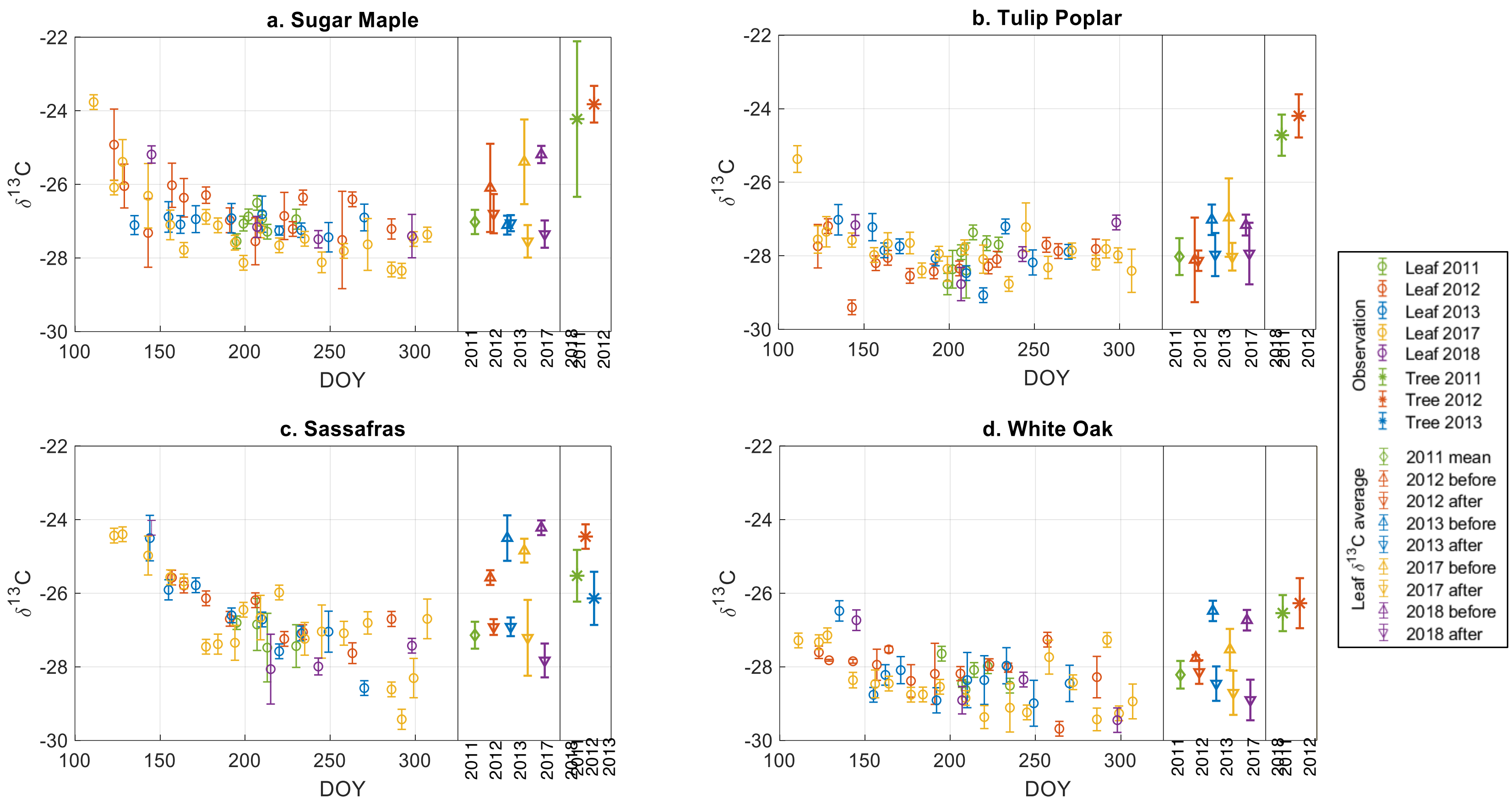
Study Site – Morgan Monroe State Forest (MMSF)

- MMSF is located 20 miles from Bloomington in Indiana, and is a secondary successional broadleaf forest
- Long term eddy covariance tower measures CO_2 and H_2O fluxes
- 75% of the basal area is comprised of Sugar Maple, Tulip Poplar, Sassafras, and Oak species

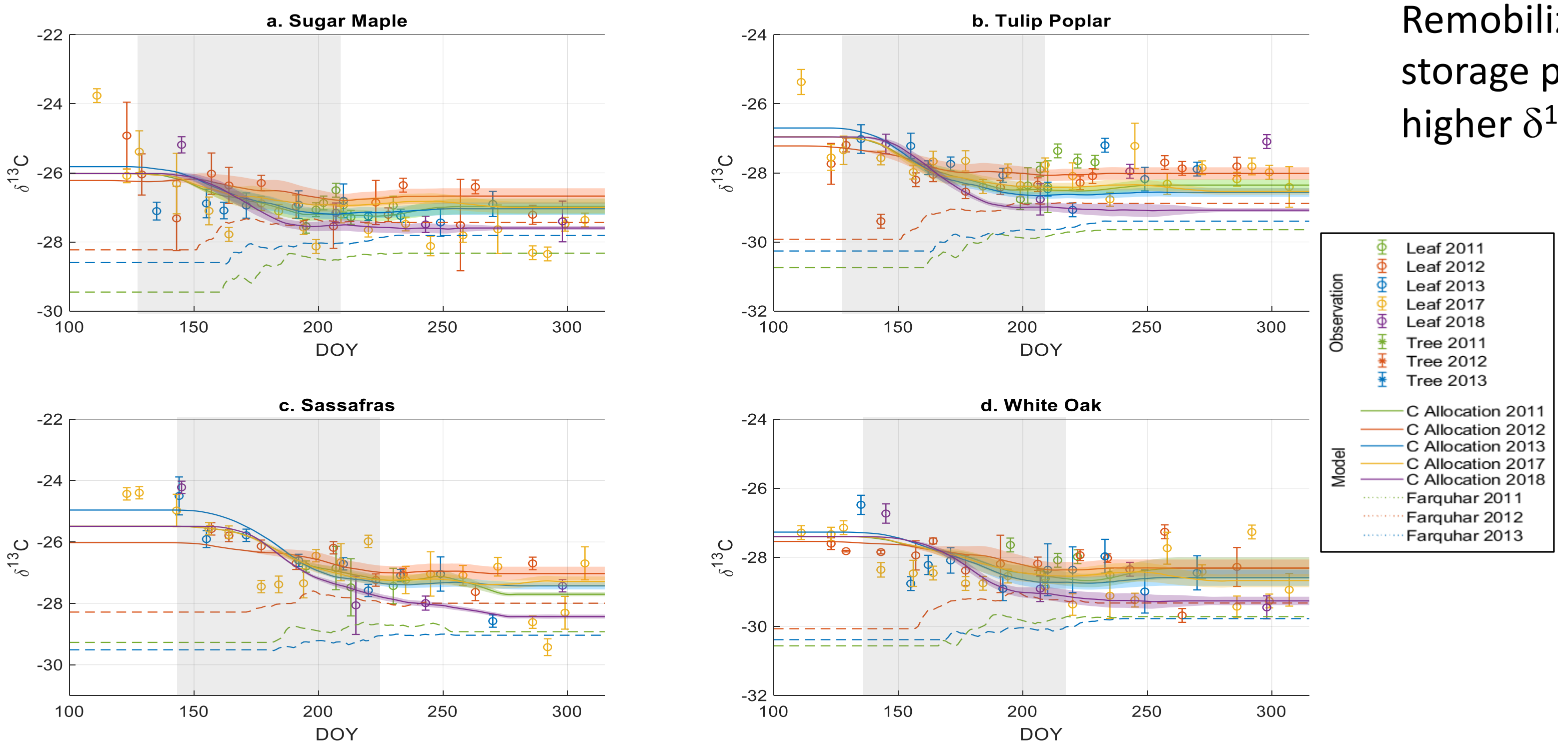


Brzostek et al., 2014; Roman et al., 2015

Leaves sampled over the growing season change $\delta^{13}C$, start enriched and get lighter.

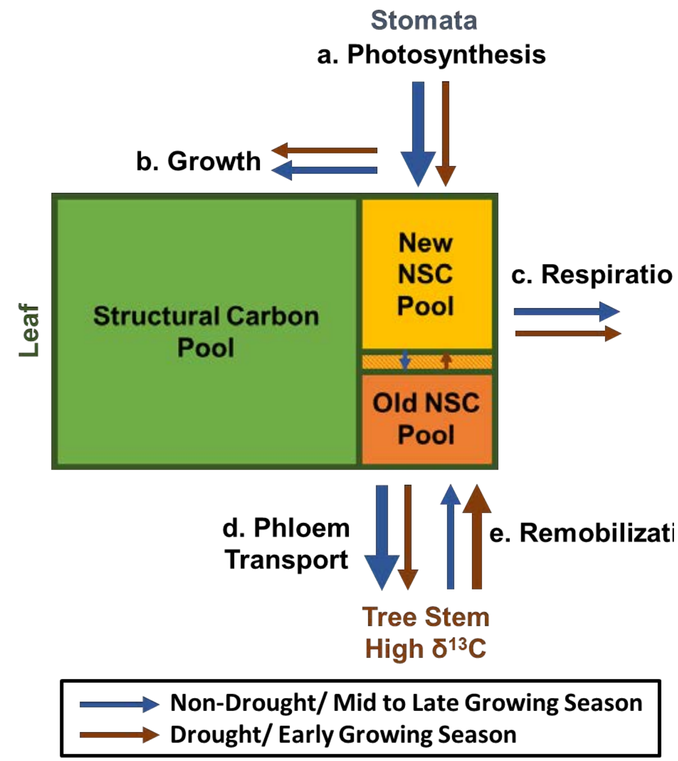


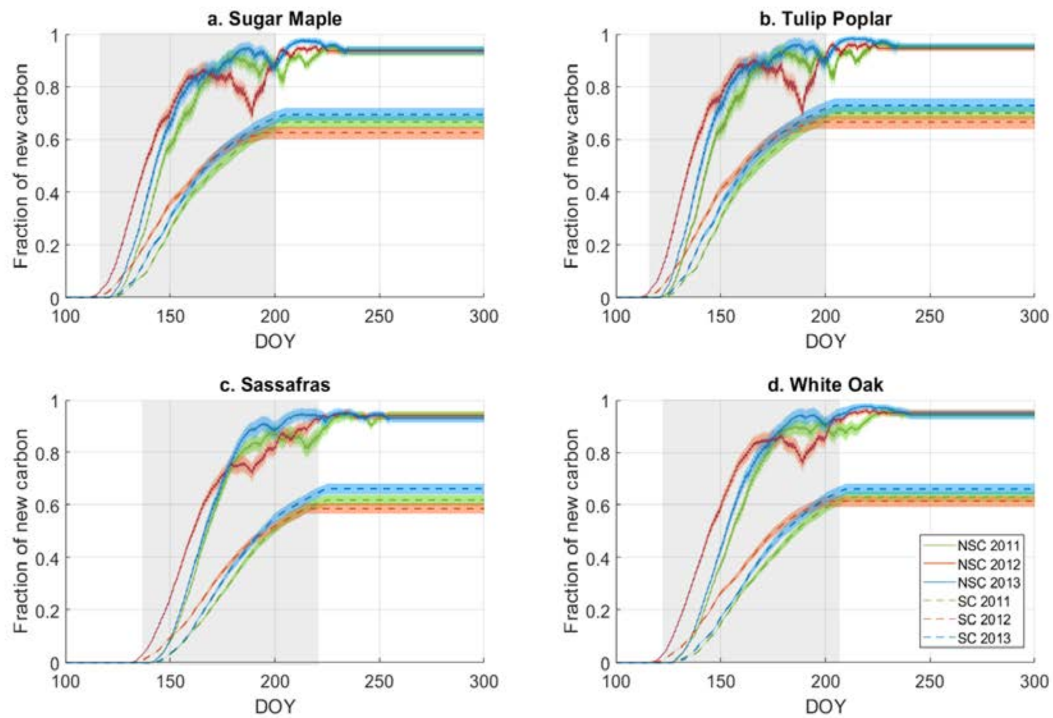
Spring leaf $\delta^{13}C$ can't be explained by photosynthetic discrimination, but rather stored carbon used for leaf flush.



Remobilized NSC from storage pools tends to have higher $\delta^{13}C$ values.

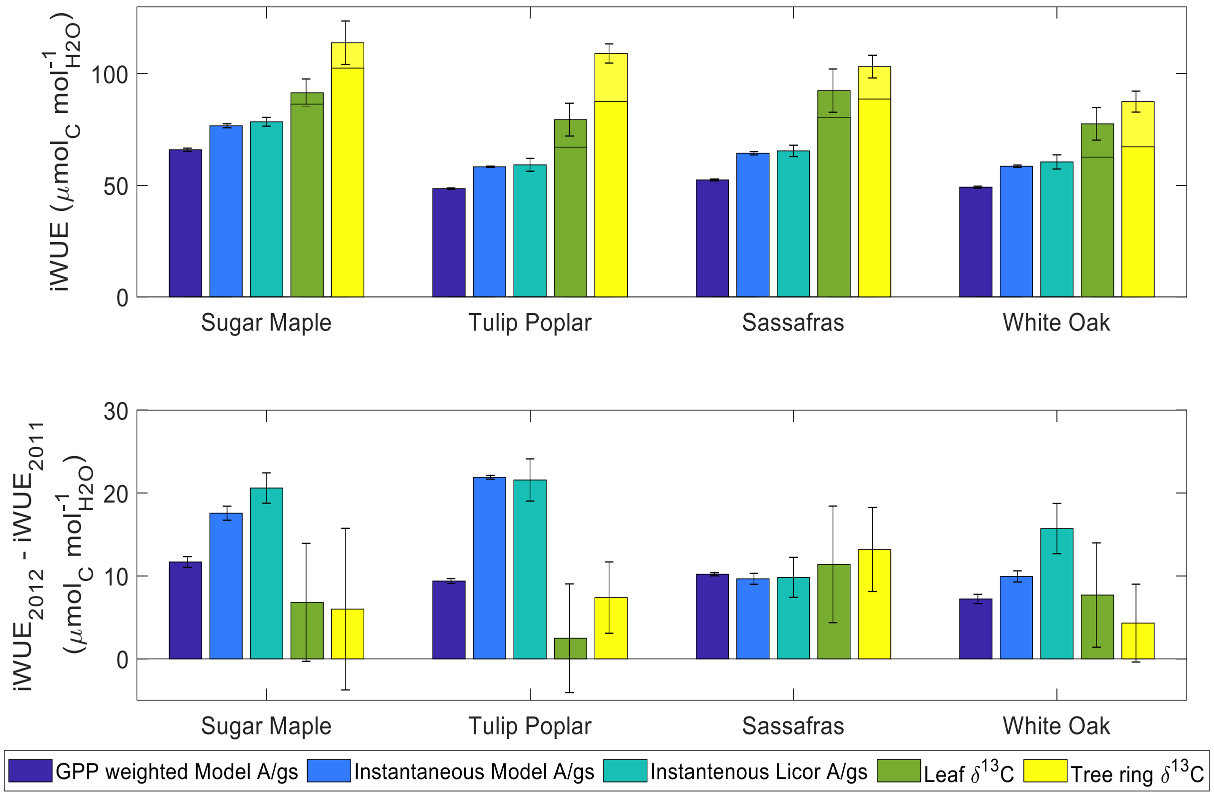
Modeled leaf carbon to track changes in $\delta^{13}C$ of leaf as they transition from old carbon to new carbon sources.





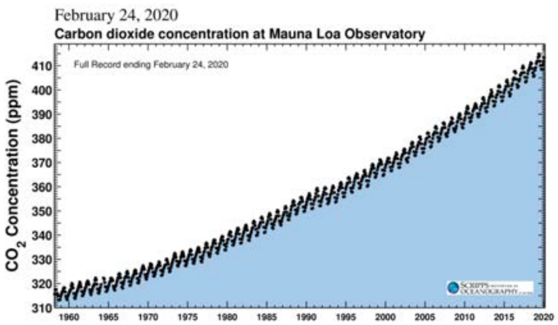
NSC = non-structural carbohydrates (sugars and starches)

Early season remobilization of stored carbon enriched in ^{13}C can explain the offset in iWUE estimates by different methods.



- Allocation of remobilized carbon can explain the differences in iWUE between methods.
- The "true" physiological iWUE values are probably lower than mid-day leaf gas exchange estimates.
- iWUE was higher in the 2012 drought, but the relative magnitudes vary by species and method.
- Note that this largely affects mean bias and and drought response; not necessarily trends in iWUE.

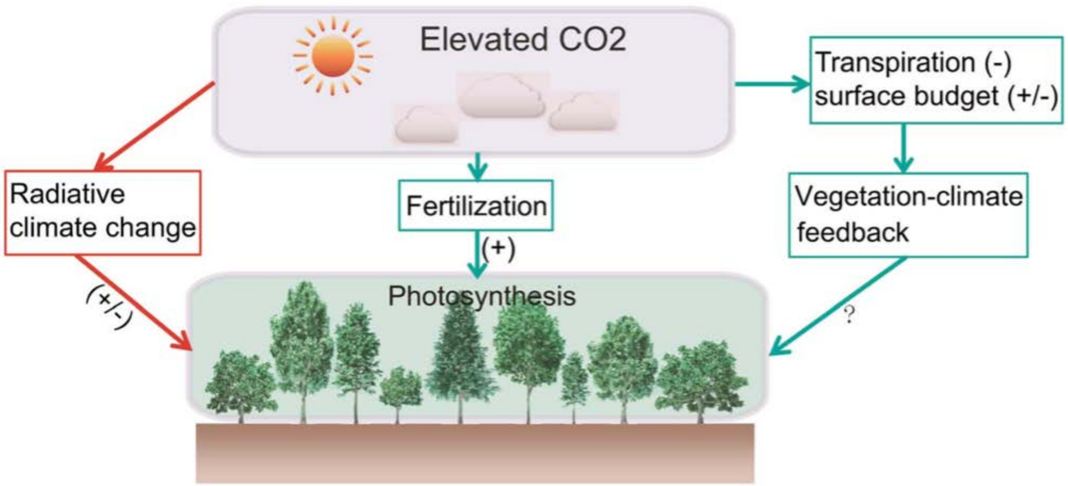
Summary



Atmospheric investigation: Trends in stomatal conductance due to increased atmospheric CO_2 concentrations. iWUE has increased in response to increasing atmospheric CO_2, maintaining nearly constant C_i/C_a ratios. Globally, the terrestrial biosphere has become less constrained by water stress.

Plant tissue investigation: Role of carbon allocation in interpreting plant tissue δ^{13}C. The use of stored carbon early in the season can explain why ^{13}C methods estimate higher iWUE than other methods in deciduous broadleaf trees. Care must be taken when using leaf (and tree-ring) δ^{13}C to validate the magnitude of iWUE in carbon cycle models, especially inter-annual variability.

Increased intrinsic WUE influences the coupled carbon-water cycle through vegetation-climate feedbacks.



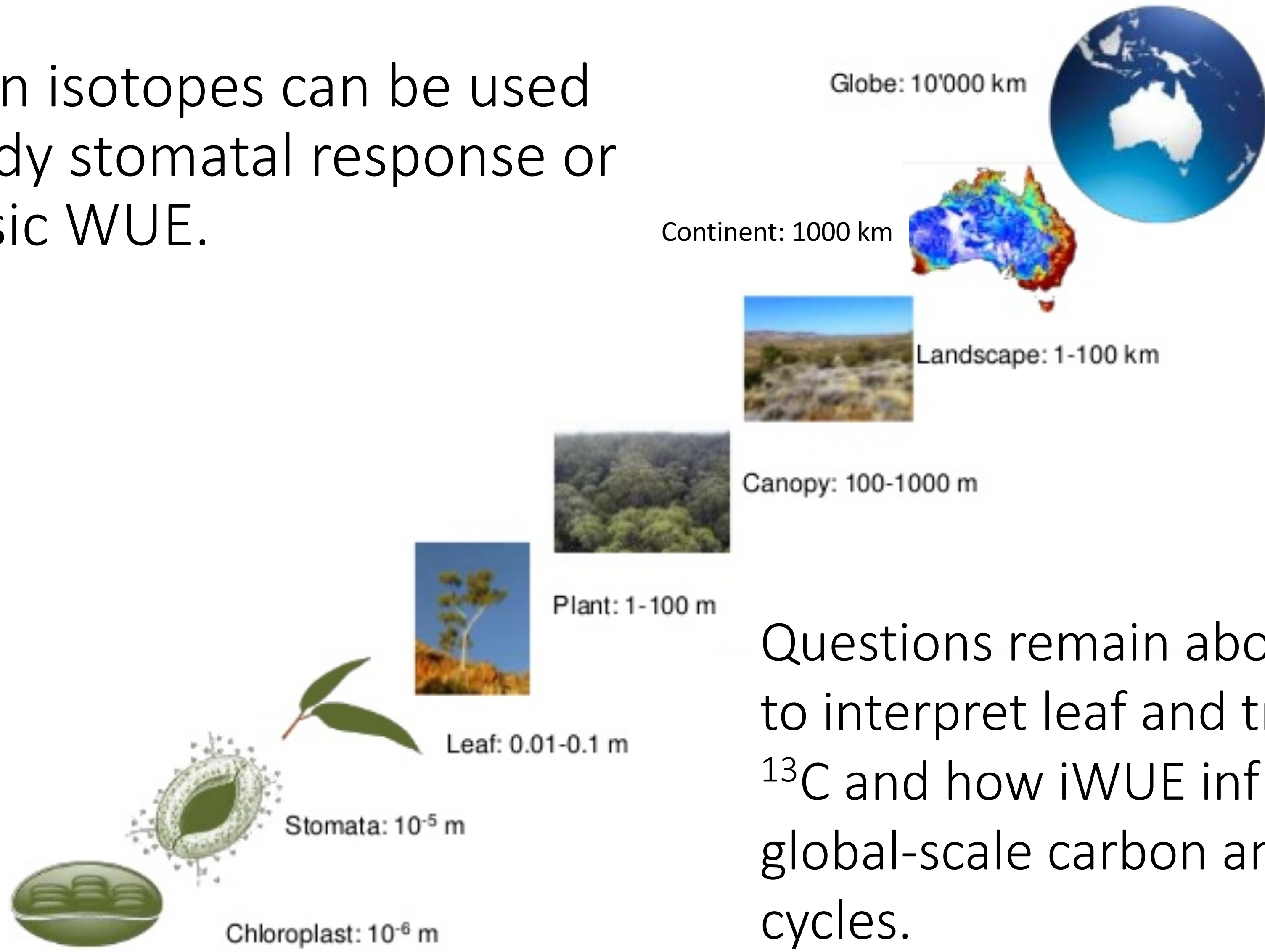
Increased intrinsic WUE could relax water stress in many plants (Choat et al., 2012).

Increased WUE may result in lower transpiration rates and precipitation thereby enhancing water stress in some regions (Zhu et al., 2017).

However, increased in leaf area and atmospheric evaporative demand may cancel these effects (Keller et al., 2017).

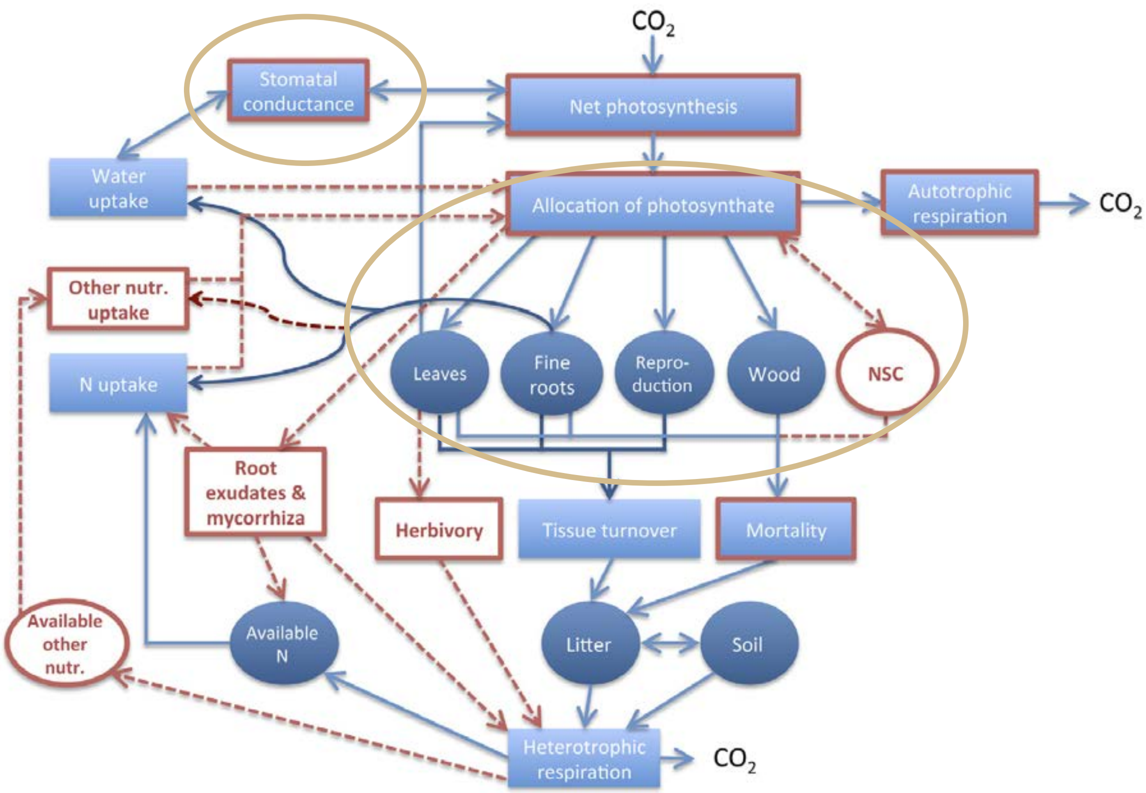
Zhu et al. including Welp (2017) Geophysical Research Letters

Carbon isotopes can be used to study stomatal response or intrinsic WUE.



Questions remain about how to interpret leaf and tree-ring ^{13}C and how iWUE influences global-scale carbon and water cycles.

Key knowledge and data gaps remain for modeling the influence of CO_2 on the terrestrial carbon sink.



Thank you to collaborators:

Ralph Keeling and Heather Graven

Youmi Oh, Kim Novick, and Koong Yi

Pugh et al., Journal of Plant Physiology, 203, 3–15, doi:10.1016/j.jplph.2016.05.001, 2016.