Is the water use efficiency of land plants changing?

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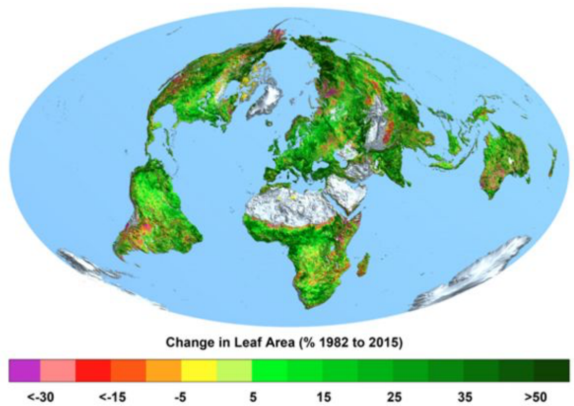

Fig. 1 % change in leaf area 1982 to 2015 estimated using remote sensing.

The globe's vegetation is closely intertwined with the global carbon and hydrological cycles thus changes in plant functioning can have substantial consequences for climate. Plants fix atmospheric CO_2 via photosynthesis into various forms of reduced organic carbon. These in turn build the basis for all functions in the plant e.g. to provide structural elements for growth (cellulose) or to provide easily transportable energy in form of sugars to maintain metabolism. Fixed organic carbon is released to the atmosphere when converted back (respired) to gaseous CO_2 via oxidation either in the plant or by microorganisms feeding on dead organic plant material. Thus imbalances between these two processes have the potential to affect atmospheric CO_2 levels substantially for example through increases in total plant mass. Such changes can be relevant at the global scale because the total amount of organic carbon in vegetation and soils is several times larger than the amount of CO_2 in the atmosphere.

Fig.2 High resolution photography of stomata.

Uptake of atmospheric CO_2 by plants is via stomata, small (~10^{-6} m length) valve-like openings located on the lower side of leaves (Hetherington & Woodward, 2003). Plants maintain below atmospheric CO_2 levels inside stomata thus on opening CO_2 will diffuse from the atmosphere into the stomata feeding the plant. In contrast evaporation of leaf water inside the intercellular space keeps intercellular air inside leaf saturated with water thus driving a loss of plant water to the atmosphere. The ratio of plant carbon gain to water lost in units of molecules per unit of time, called water use efficiency (WUE), is typically on the order of 1/200-1/500. Thus soil water loss per carbon gained is large and tends to be a limiting factor for plant growth. Therefore plants need to be economical with water.

Plants access water primarily via their roots, from where water is pulled to the leaves where it is lost to the atmosphere via transpiration through stomata when they take up carbon. Because of this link plants act as water pumps from the soil to the atmosphere recycling several times per year the amount of water in the atmosphere (Hetherington & Woodward 2003). In this way vegetation influences significantly precipitation in inland areas (Spracklen et al 2012). A second implication of changes in plant functioning, and specifically water use efficiency, is therefore to affect the hydrological cycle.

Plant growing conditions on our planet are changing. The key ingredient for plant growth, atmospheric CO_2, has increased by nearly 50 percent compared to pre-industrial levels and keeps raising. Because of greenhouse warming land temperatures steadily increase, and precipitation and humidity patterns are changing. It is thus expected that plants will react and adapt their habits of functioning. One main expected effect is changes in water use efficiency, WUE, which at the leaf level, and assuming steady state, can be expressed as

$$WUE \equiv \frac{CO_2 \text{ gain by leaf}}{H_2O \text{ loss by leaf}} = \frac{\frac{c_a - c_i}{g_{CO2}}}{\frac{e_i - e_a}{g_{H2O}}} = \frac{\frac{1}{g_{CO2}} c_a \left(1 - \frac{c_i}{c_a}\right)}{\frac{VPD}{g_{H2O}}} \equiv \frac{WUE_i}{\frac{VPD}{g_{H2O}}}$$

Here c_a and c_i are, respectively, CO_2 mixing ratio in atmosphere and inside stomata, e_a and e_i the same but for water vapour, g_{CO2} and g_{H2O} stomatal conductivity for CO_2 and H_2O, and $VPD \equiv (e_i - e_a)$ is vapour pressure deficit (leaf internal vapour e_i is assumed to be at saturation). Gross primary productivity of vegetation is the amount of carbon taken up by plants and thus this relationship can be rearranged to

$$GPP_{leaf} = \frac{Transp}{\frac{VPD}{g_{H2O}}} WUE_i$$

where $Transp \equiv \frac{e_i - e_a}{g_{H2O}}$ is transpiration. Thus if all else remains equal, increased levels of atmospheric CO_2 need less opening(s) of stomata to obtain the same amount of carbon (i.e, keep gross primary productivity, GPP constant). Alternatively, plants may not change their stomatal opening(s), thus possibly leading to greater carbon uptake. Both changes are observed: plants change stomatal conductance under higher CO_2 through either dynamic closure of stomata or changes in stomatal density, and/or changes in leaf size, and plants grow faster under higher CO_2, possibly explaining the residual carbon sink into vegetation in many biomes (Pan et al. 2011). Higher CO_2 leads further to shifts in boundaries between forests and savannahs in the tropics, as most grasses lose their competitive advantage resulting from their higher efficiency of their photosynthesis pathways in a low CO_2 world. The latter is indeed being observed.

If plant productivity and plant-to-atmosphere vapour deficit stayed the same, then an increase in water use efficiency would have various observable effects on the hydrological cycle (e.g. Gedney et al. 2006). At the large hydrological catchment scale (like e.g. the Amazon basin), reduced recycling of soil water back into the atmosphere would lead to an overall decrease in water vapour in the atmosphere and thus a likely decrease in precipitation, with cumulatively increasing effect on vegetation along the main airstream (Spracklen et al. 2012). Finally total river discharge out of the catchment (e.g. Amazon river discharge to the Atlantic) would remain the same but peak runoff times would change. Recent observed changes in the Amazon river discharge (Gloor et al. 2013) may indeed be partially explained by such effects.

Because of its importance both for predicting global carbon cycle and the hydrological cycle on land in the future, it is of great interest to have a clear understanding whether WUE and WUEi are indeed changing. Various methods have been employed to measure changes in water use efficiency – often via a focus on WUEi - because a mechanism based model suggests a link between $^{13}CO_2$ carbon isotope difference between atmosphere and plant, and the $^{13}CO_2/^{12}CO_2$ ratio of organic material can be measured fairly easily and with high accuracy. Plants discriminate against $^{13}CO_2$. Plant material is therefore depleted in the heavy $^{13}CO_2$ isotope of CO_2. Nonetheless the level of discrimination depends on how widely stomata open on average. Specifically, according to the standard model, the difference of isotopic ratio in air and plant is a weighted mean of a small fractionation caused by diffusion, the dominant process if stomata are nearly closed, and a large fractionation during carboxylation, dominant when stomata are wide open. Thus the level of $^{13}CO_2$ discrimination in plant material provides a measure of how much stomata are closed. Time trends of $^{13}CO_2$ discrimination, from e.g. tree rings, or herbarium material, are therefore indicative of plant responses over time to CO_2 increases.

Approach

While there have been many attempts to determine robustly changes in plant WUE, methodological issues have prevented firm conclusions. For example methods based on tree cores tended to fail to control for life-stage effects (Brienen et al. 2017). This project aims to produce firm conclusions about changes in WUE (WUEi) in vegetation by using three lines of investigation which when combined together should provide a more convincing assessment of this question than has been possible sofar.

Firstly we propose to analyse precipitation and riverine discharge records of selected large basins in the world, like the Amazon basin, to establish to what extent changes in discharge and precipitation patterns are consistent with changes in forest water use efficiency.

Secondly we propose to build on work by various others including Ralph Keeling to explore what the global atmospheric $^{13}CO_2$ record reveals about changes in vegetation isotopic discrimination over. Atmospheric $^{13}CO_2$ is steadily decreasing because fossil fuel $^{13}CO_2$ is depleted but the rate of decrease seems to be smaller than expected based simple carbon cycle box models of atmosphere, oceans and land vegetation. We propose to follow up on these analysis using similarly simple models.

Finally while naïve use of tree core based isotope records will not yield reliable estimates of water use efficiency changes a more sophisticated approach may be feasible. Trying to devise and apply more reliable methods based on such data, possibly also involving herbarium and/or a field work component will be pursued.

References

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