



Observations and scaling of water use efficiency from leaf to globe

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Water use efficiency (WUE) defines the ratio of plant carbon gain to water loss and provides a critical link between carbon and water cycles in terrestrial ecosystems. Understanding this link is central to assessing how plants and ecosystems respond to climate change. At the leaf level, WUE is often assessed using stable carbon isotopes, which relates most directly to the ratio of net assimilation (A) to stomatal conductance (g). Although stable isotopes are useful for assessing time-averaged A/g , they are difficult to quantify at canopy or larger spatial scales. Leaf gas exchange can provide direct measurements of A and g and therefore provides information on the causes of variation in WUE, yet, it is generally limited to individual leaves at instantaneous time-scales. Eddy covariance can provide measures of gross primary productivity (GPP) and evapotranspiration (ET) at the whole ecosystem scale and on a near-continuous basis, but the physiological interpretation of the ratio GPP/ET as WUE can be confounded by the presence of soil evaporation (E). Recent advances in remote sensing of both photosynthesis (A) and canopy transpiration (T) now make it possible to estimate WUE as the ratio of A/T at regional to global scales, but validation of these and other synoptic scale estimates is limited by the lack of comparable observations. Reconciling the differences among stable isotope, leaf gas exchange and eddy covariance estimates of WUE is needed to provide the necessary data for validating such upscaling methods and to understand the mechanisms underlying variation in WUE at different spatial scales, from leaves to canopies to the globe.

Using observations in a Mediterranean oak savanna of California, we compared estimates of WUE at leaf, canopy and ecosystem scales based on stable carbon isotopes, leaf gas exchange, eddy covariance and remote sensing. Leaf level estimates for individual trees were based on the carbon isotope composition ($\delta^{13}C$) of recently fixed carbohydrates (leaf soluble sugars) as well as bulk leaf tissue. Leaf level estimates were also made based on gas exchange measurements of net photosynthesis and stomatal conductance. Canopy level estimates were based on the ratio of canopy net photosynthesis and transpiration determined as the difference between above- and below-canopy eddy fluxes. Ecosystem level estimates were based on the ratio of eddy flux measures of GPP to ET. Finally, we compared these 'observed' values of leaf, canopy and ecosystem WUE to those based on remote sensing estimates of canopy photosynthesis and transpiration. We then applied the remote sensing approach to estimate global scale spatial patterns in WUE.

The stable carbon isotope composition of leaf soluble sugars was found to be a more robust measure of short term WUE and its seasonal variation than bulk leaf carbon because sugars reflect the initial isotopic discrimination during gas exchange, without the confounding effects ascribed to storage, tissue chemical composition and time of tissue formation. Intra- and inter-annual variation in A/g based on sugar isotopes indicated coordinated adjustment in A and g during the growing season in 'wet' years, while in 'dry' years, A/g increased during drought. WUE based on leaf gas exchange was more consistent with estimates based on canopy eddy flux than sugar isotopes, potentially due to the influence of mesophyll conductance that is captured by the isotopes but not by gas exchange methods. Trends in A and g from leaf gas exchange indicated that the increase in A/g during dry years was due primarily to a decrease in g during the initial stages of drought, with coordinated changes in A and g thereafter. Remote sensing estimates of GPP and ET were consistent with values determined by eddy flux. Further, remote sensing estimates of WUE based on the ratio of A/T were more consistent with those based on leaf gas exchange and tree canopy eddy flux than isotopes. Work is underway to determine the impact of soil evaporation (E) on estimates of WUE based on eddy flux at the ecosystem scale. Finally, satellite-based estimates of WUE are discussed in relation to global spatial patterns of vegetation type and meteorological conditions.