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Capturing species-level drought responses in a temperate deciduous forest using ratios of photochemical reflectance indices between sunlit and shaded canopies

Taehee Hwang[a,*,1], Hamed Gholizadeh[a,1], Daniel A. Sims[a,1], Kimberly A. Novick[b], Edward R. Brzostek[c,d], Richard P. Phillips[c], Daniel T. Roman[b,e], Scott M. Robeson[a], Abdullah F. Rahman[a,f]

[a] Department of Geography, Indiana University Bloomington, Bloomington, IN 47401, USA
[b] School of Public and Environmental Affairs, Indiana University Bloomington, Bloomington, IN 47401, USA
[c] Department of Biology, Indiana University Bloomington, Bloomington, IN 47401, USA
[d] Department of Biology, West Virginia University, Morgantown, WV 26506, USA
[e] U.S. Department of Agriculture, Forest Service, Northern Research Station, Grand Rapids, MN 55744, USA
[f] Coastal Studies Lab, University of Texas Rio Grande Valley, South Padre Island, TX 78597, USA

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ABSTRACT

To classify trees along a spectrum of isohydric to anisohydric behavior is a promising new framework for identifying tree species' sensitivities to drought stress, directly related to the vulnerability of carbon uptake of terrestrial ecosystems with increased hydroclimate variability. Trees with isohydric strategies regulate stomatal conductance to maintain stationary leaf water potential, while trees with anisohydric strategies allow leaf water potential to fall, which in the absence of significant hydraulic cavitation will facilitate greater rates of carbon uptake. Despite the recognition of the gas exchange consequences of isohydric and anisohydric strategies for individual tree species, there have been few studies regarding whether isohydric trees produces distinct spectral signatures under drought stress that can be remotely sensed. Here, we examined the capability of four vegetation indices (PRI, NDVI, $NDVI_{705}$, and EVI) to capture the differences in spectral responses between isohydric and anisohydric trees within a deciduous forest in central Indiana, USA. Both leaf-level spectral measurements and canopy-scale satellite observations were used to compare peak growing-season spectral signatures between a drought and a non-drought year. At the leaf scale, two vegetation indices (NDVI and $NDVI_{705}$) failed to capture the drought signal or the divergent isohydric/anisohydric behavior. EVI successfully captured the drought signal at both leaf and canopy scales, but failed to capture the divergent behavior between isohydric and anisohydric tree species during the drought. PRI captured both drought signals and divergent isohydric/anisohydric behavior at both leaf and canopy scales once normalized between sunlit (backward direction images) and shaded (forward direction images) portions of canopy, which indicates drought stress and subsequent photosynthetic down-regulation are greater in the sunlit portion of canopy. This study presents a significant step forward in our ability to directly mapping emergent isohydricity at different scales based on divergent spectral signatures between sunlit and shaded canopies.

1. Introduction

Recently, many forested regions in the United States have experienced increasing drought stress under ongoing climate change (Dai, 2013). Warmer temperatures have increased hydroclimate variability (Seager et al., 2009; O'Gorman and Schneider, 2009) with more frequent droughts, contributing to acute reductions in net ecosystem productivity (Roman et al., 2015), prolonged water stress (Brzostek et al., 2014; Xu and Baldocchi, 2003), and widespread tree mortality (Adams et al., 2009; Allen and Breshears, 2007; McDowell and Allen, 2015) in forested ecosystems. Differences between tree species in their response to imposed hydrologic stress can be evaluated by characterizing species along a continuum of isohydric to anisohydric behavior (Choat et al., 2012; Klein et al., 2014; Martinez-Vilalta et al., 2014).

* Corresponding author.
E-mail address: taehee@indiana.edu (T. Hwang).
[1] These three authors equally contributed to the paper.

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Despite the risk of xylem cavitation associated with highly negative leaf water potentials, trees with anisohydric strategies frequently sustain high stomatal conductance during drought (Matheny et al., 2017; Meinzer et al., 2017; Roman et al., 2015; Yi et al., 2017). In the absence of significant xylem cavitation, this strategy can also support relatively high levels of photosynthesis during periods of drought stress. In contrast, trees with isohydric strategies regulate stomatal conductance to maintain a relatively stationary leaf water potential as soil moisture declines. This strategy reduces embolism risk, but at a cost of reduced carbon assimilation (McDowell et al., 2008). The ratio of drought-driven declines in carbon uptake as compared to stomatal conductance depends on the plasticity of the plant's intrinsic water use efficiency, which can increase during periods of hydraulic stress, but not typically to an extent to completely mitigate losses in carbon uptake linked to stomatal closure (Novick et al., 2015). In relatively mesic forests like Eastern US, where drought events can have large effects on carbon and water cycling but rarely cause extensive hydraulic failure, the isohydric/anisohydric continuum is well suited for predicting the extent to which trees regulate their stomates during drought periods (Novick et al., 2015; Roman et al., 2015; Yi et al., 2017), as well as the resulting carbon assimilation strategies. The sensitivity of gross primary production (GPP) to drought stress has been shown to depend strongly on the relative proportion of isohydric vs. anisohydric tree species in forest stands (Roman et al., 2015). Recent works also suggest that isohydric stands are associated with greater interannual variability of evapotranspiration and reduced productivity compared to anisohydric stands, as related to strong isohydric behavior in their stomatal control and cavitation vulnerability (Ford et al., 2011; Novick et al., 2016; Stoy et al., 2006). As a result, the degree to which forest stands respond isohydrically or anisohydrically to drought stress directly influences ecosystem productivity and has the potential to cause cascading effects on regional carbon storage.

While diagnosing isohydric vs. anisohydric stomatal responses is relatively straightforward, albeit labor-intensive, at the tree level (Meinzer et al., 2016), we have little understanding of how this behavior can be detected at large scales using remote sensing data. Specifically, there has been limited research regarding whether isohydric and anisohydric trees possess distinct spectral responses under drought stress (Sims et al., 2014) that can be remotely sensed and mapped to parameterize large-scale GPP models (Konings and Gentine, 2016; Sperry et al., 2016). Classically, light use efficiency (LUE) based GPP models have been widely used to assess the impact of droughts on carbon sequestration at a global scale (e.g. Song et al., 2013). In these models, GPP is usually proportional to the multiplicative term between LUE and absorbed photosynthetically active radiation (APAR). However, remote sensing metrics of canopy greenness often fail to capture small changes in leaf area or its function (i.e. stomatal closure) that accompany drought (Asner et al., 2004; Hwang et al., 2008; Sims et al., 2014). For this reason, most remote-sensing based terrestrial productivity models use water stress functions that downregulate LUE values under conditions of low water availability, based on either vapor pressure deficit (VPD) or soil moisture metrics (Song et al., 2013). These models are often applied to a wide range of vegetation composition and formulate the stomatal responses with a single set of ecophysiological model parameters based on the major plant functional types (e.g. Biome Parameter Look-Up Table for MODIS GPP; Zhao et al., 2005). Consequently, current model structures cannot reproduce observed differences in drought sensitivity among isohydric and anisohydric species within temperate deciduous forests. This mismatch between our theoretical understanding of plant drought response and its representation in models highlights a critical knowledge gap in understanding the vulnerability of carbon sequestration of terrestrial ecosystems under increased hydroclimate variability, especially in terms of species-specific variability with different water use and carbon assimilation strategies under drought conditions.

Recently, there have been advances in directly mapping LUE using imaging spectroscopy from different platforms. LUE mapping using remote sensing data is mostly based on the detection of excess energy not used in photosynthesis especially under drought conditions (Coops et al., 2010; Demmig-Adams and Adams, 1996), using the photochemical reflectance index (PRI) (Gamon et al., 1992; Gamon et al., 1997; Penuelas et al., 1995). PRI has been successfully applied across various remote sensing platforms ranging from narrow bandwidth spectro-radiometers to the Moderate Resolution Imaging Spectroradiometer (MODIS) (Drolet et al., 2008; Drolet et al., 2005; Goerner et al., 2009). Although PRI values are closely related to photosynthetic LUE values across different scales (see Garbulsky et al., 2011), PRI-LUE relationships often show strong sensitivity to shadow fractions following sun-target-sensor geometry (Drolet et al., 2005; Hall et al., 2008; Hilker et al., 2008), as well as canopy structures and soil background reflectance (Barton and North, 2001; Suárez et al., 2008). Across forest ecosystems, the correlation between LUE and PRI for sunlit canopy is higher than shaded canopy during water-stress conditions (Hall et al., 2008; Zhang et al., 2016). Expanding on this framework, known correlations between view angle and canopy LUE suggest that the variability in PRI values with view angle is directly related to the degree of down-regulation between sunlit and shaded portions of the canopy (Coops et al., 2010; Drolet et al., 2005). Using multi-angle satellite systems, such as backward and forward direction images, to capture the sunlit and shaded portion of canopy, respectively (Hall et al., 2012; Hall et al., 2008), it may be possible to derive canopy responses to drought (i.e. isohydry vs. anisohydry) by quantifying the extent to which sunlit and shaded canopies differ in PRI.

In this paper, we hypothesize that the degree to which canopies downregulate photosynthesis under drought stress (isohydry vs. anisohydry) is directly correlated with the magnitude of the differences in PRI between sunlit and shaded portions of canopy (Coops et al., 2010). Further, using both leaf and canopy scale measurements, we seek (1) to capture the difference in leaf-scale spectral signatures between isohydric and anisohydric trees species under drought stress, and (2) to examine whether this behavior can be detected at the canopy scale using multi-angle MODIS images. To meet these objectives, we combined site-level spectral observations and remotely sensed data for a biologically diverse temperature deciduous forest that contains a broad spectrum of isohydric and anisohydric species, and that experienced an exceptionally severe drought in 2012 (Roman et al., 2015).

2. Methods and materials

2.1. Study area

The study site is located in the Morgan Monroe State Forest (MMSF; 39.3232°N, 86.4131°W) in central Indiana, USA. MMSF is a deciduous broadleaf forest with average canopy height and rooting depth of 27 m and 0.44 m, respectively (Ehman et al., 2002). Among the common tree species found in the study region, sugar maple (*Acer saccharum*), tulip poplar (*Liriodendron tulipifera*) and sassafras (*Sassafras albidum*) are generally recognized to be among the most isohydric (or conservative) species, whereas white and red oaks (*Quercus alba* and *Q. rubra*) are anisohydric (or non-conservative) (Choat et al., 2012; Novick et al., 2015; Roman et al., 2015). Based on measurements of trees with diameter at breast height ≥ 10 cm made in 54 large plots in March 2011, the study site is dominated by isohydric species such as sugar maple, tulip poplar and sassafras, which represent 21%, 25%, and 10% of total basal area, respectively, while the anisohydric white and red oaks represent 5% and 3%, respectively. The study site experienced a severe drought during the summer (June–August) of 2012. During this time period, the total rainfall was 135 mm, which is < 50% of average June–August rainfall (302 mm from 1999 to 2015 except for 2012) (Fig. S1; June and July rainfall was just ~10% of the long-term mean). As a result, there was a dramatic early dry down of soil water content in 2012 (Fig. 1). In field measurements and remote sensing analyses, we