# DIURNAL AND SEASONAL PROXIMALLY SENSED PHOTOCHEMICAL REFLECTANCE INDEX (PRI) IN A HIGH-STRESS SEMI-ARID MIXED CONIFER FOREST.

by

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As members of the Master's Committee, we certify that we have read the thesis prepared by Julia Yang, titled *Diurnal and seasonal proximally sensed photochemical reflectance index (PRI) in a high-stress semi-arid mixed conifer forest,* and recommend that it be accepted as fulfilling the dissertation requirement for the Master's Degree.

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Final approval and acceptance of this thesis is contingent upon the candidate's submission of the final copies of the thesis to the Graduate College.

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# Abstract

A lack of accurate, reliable data on coupled carbon and water fluxes for Earth's expansive ecosystems remains a major barrier to a complete understanding of the terrestrial carbon cycle. The remotely sensed Photochemical Reflectance Index (PRI) measures deepoxidation of the xanthophyll cycle at wavelength 531nm and is one of the few pigment-based vegetation indices sensitive to rapid plant physiological responses. PRI presents new opportunities to study ecosystems on a diurnal time scale, as well as seasonal processes in evergreen systems where complex vegetation dynamics are not reflected by small annual changes in chlorophyll content or leaf structure. However, systematic PRI acquisition in conjunction with leaf and ecosystem flux measurements are needed in natural, diverse ecosystems. The growing field of proximal remote sensing affords the opportunity to bridge leaf, canopy and ecosystem scales, for a physiological inspection of whole ecosystem dynamics. The Southwest U.S. provides a natural setting for examining the influence of environmental drivers on the productivity of drought-sensitive forests, as well as for evaluating our ability to track these relationships using optical methods. We studied PRI in a semi-arid, sub-alpine mixed conifer forest, in order to assess its ability to serve as a proxy for dynamic photoprotection. We combined canopy spectral measurements with eddy covariance flux and sap flow methods to determine the sensitivity of PRI to seasonal changes in gross primary productivity (GPP) and the ecohydrological variability of a high stress environment. In addition, we combined top-of-canopy leaf-level gas exchange, chlorophyll fluorescence, and hyperspectral measurements to determine the sensitivity of PRI to diurnal changes in needle photosynthetic function, and confirm the extent to which canopy diurnal patterns reflect leaf physiology. At the canopy scale we found that the relationship between PRI and GPP was inconsistent over the course of the monsoon season, shifting from a negative relationship in July and August ($R^2$=.62), to a positive relationship in September ($R^2$=.48). Multiple linear regression with soil moisture and air temperature showed that PRI responded to dynamic water and energy limitations of this system ($R^2$=.41). We report for the first time a relationship between seasonal PRI and sap flow in a natural forest ($R^2$=.55). These results suggest that on a seasonal scale PRI is an effective indicator of photosynthetic response to ecohydrological constraints. On a diurnal scale we found that PRI remained constant throughout the day at both leaf and canopy scales, and we suggest that saturated light conditions drive retention of xanthophylls in a de-epoxidized state. We contribute evidence that remotely sensed PRI has potential to fill a major gap in our ability to distinguish how water availability influences forest productivity and associated carbon dynamics.

# 1. INTRODUCTION

## *1.1 Background*

Accurate modeling of the global carbon (C) cycle is critical for understanding and predicting a wide range of feedbacks between climate and the terrestrial biosphere. For example, climatic factors are important drivers of ecosystem productivity, which in turn, feeds back to influence local and regional climate (Beer et al. 2010; Bonan 2008; Schimel et al. 2015). Overall, terrestrial ecosystems are a net C sink, meaning they uptake roughly a quarter of anthropogenic carbon dioxide ($CO_2$) emissions (Le Quere et al. 2016), and small variations in ecosystem function can have large implications for the strength of the terrestrial C sink (Le Quere et al. 2009). Estimating terrestrial carbon uptake, referred to as gross primary productivity (GPP), is a major goal of Earth systems science. Although significant advancements have been made in our ability to model GPP (Beer et al. 2010; Makela et al. 2008; Piao et al. 2013), it remains an ongoing challenge for ecologists to provide high-quality data and reduce errors in uncontrolled field settings.

A complete understanding of the terrestrial C cycle depends on our ability to understand seasonal changes in photosynthetic function, and how these are correlated with environmental constraints across time. Net photosynthesis can be quantified at the ecosystem level using towers with eddy covariance (EC) flux methods (Baldocchi 2008), which have proven especially useful because they integrate over spatial heterogeneity within a canopy and take measurements continuously through time. However, while these methods tell us a great deal about $CO_2$ and water exchange between the biosphere and atmosphere, many questions remain unanswered due to the black-box nature of these fluxes. To gain a mechanistic understanding of how plant function drives these patterns, leaf-level analysis of gas exchange can be performed using chamber enclosure systems (Long and Bernacchi 2003). In turn, these methods gain physiological depth at the expense of spatiotemporal coverage. While field methods at the leaf and canopy scale are irreplaceable in the type of information provided, these are expensive, time intensive, and reinforce the problematic data bias towards locations with ease of access. Thus, for decades, remote sensing studies have provided estimates of vegetation productivity from ecosystem to global scales (Field et al. 1995; Jung et al. 2011; Prince and Goward 1995; Running et al. 2004; Schimel et al. 2015), providing critical input for Earth system models.

Interannual variability of the global C sink is dominated by functional variation of arid and semi-arid ecosystems (Ahlstrom et al. 2015), which are highly sensitive to precipitation inputs and climate anomalies (Scott et al. 2015). However, remotely sensed data largely fails to capture this variability (Biederman et al. 2017), introducing systematic error into C cycle models, especially during prolonged dry periods (Keenan et al. 2012). Therefore, improving the capability of remote sensing to monitor C flux response to hydrologic variability is needed. In particular, this is important for monitoring and predicting changes in montane forests across the western U.S., which account for the majority of $CO_2$ uptake in the region (Schimel et al. 2002). These forests are already sensitive to changing water availability (Monson et al. 2002) and are projected to experience severe increases in drought under future climate scenarios (Williams et al. 2013). Yet, we have an incomplete understanding of forest decline due to drought (Allen et al. 2010), and our ability to model tree-water relations is limited by a lack of robust methodology for measuring coupled C and $H_2O$ fluxes on large scales. These gaps in our knowledge are becoming increasingly critical to address, as widespread water stress is projected to increase under future warming (Garfin et al. 2013) and has already been shown to drive unprecedented reductions in continental scale C sequestration (Ciais et al. 2005). The ongoing heat-driven drought makes the Southwest U.S. a natural setting for examining the influence of environmental drivers on the productivity of drought-sensitive forests (Seager et al. 2007; Udall and Overpeck 2017), as well as evaluating our ability to track these relationships using optical methods.

Methods of estimating GPP from remotely sensed products have been predominately based on the light use efficiency (LUE) model originally developed by John Monteith (Monteith 1972, 1977). The LUE model has been the paradigm in remote sensing to evaluate GPP on ecosystem to global scales (Field et al. 1995; Hilker et al. 2008), and is presented as:

$$\text{GPP} = \text{APAR} * \text{LUE}$$

$$\text{APAR} = \text{fAPAR} * \text{PAR}$$

Where LUE is the light use efficiency term, and APAR is the absorbed photosynthetically active radiation (PAR) – equal to the total amount of PAR times the fraction absorbed by the canopy (fAPAR). For better or for worse, this extremely simple equation attempts to encompass a complex tangle of biological processes. Physiologically, APAR measures the maximum *potential* photosynthesis*,* while LUE is an adjustment for how much of that potential is actually realized due to less-than-ideal environmental conditions (Gamon et al. 2015). While fAPAR is a biophysical term that represents long-term variability in vegetation structure and composition, LUE is a functional term that reflects short-term variability in physiological responses to a dynamic environment (Porcar-Castell et al. 2014). Typically, indices based on leaf pigment and structure reflectance properties such as the Enhanced Vegetation Index (EVI) and Normalized Difference Vegetation Index (NDVI) have been used to estimate changes in the fAPAR term of the LUE model (Goward and Huemmrich 1992; Myneni et al. 1997; Myneni and Williams 1994; Sellers 1985), while assuming that LUE is constant or making adjustments based on sparse meteorological data. However, it has been shown that LUE is far from constant (Gamon et al.

1992; Sinclair and Muchow 1999) – it varies over time and space, and allowing LUE to vary improves estimation of GPP (Rossini et al. 2010).

LUE is controlled by a diverse and complex set of photoprotective processes that work in concert to downregulate photosynthesis, and the biology of these processes and their interactions are not fully understood even at the thylakoid level. When a plant absorbs light energy in excess of what can be used to drive electron transport in the light reactions of photosynthesis, it must dissipate energy that would otherwise cause photo-oxidative damage (Barber and Andersson 1992; Demmig-Adams and Adams 2000). This energy dissipation can occur through various mechanisms, but the primary pathway is through non-photochemical quenching (NPQ) via xanthophyll pigments (Demmig-Adams and Adams 1992, 1996; Muller et al. 2001). Xanthophylls, a major division carotenoid pigments, regulate flexible NPQ processes, which operate on diurnal time scales and reset each night (Demmig-Adams and Adams 2006; Muller et al. 2001; Porcar-Castell 2011). Xanthophyll pigments have three forms – violaxanthin (V), antheraxanthin (A), and zeaxanthin (Z) –that can be interconverted through enzymatic reactions involving an epoxy group. During times of excess light energy, V is de-epoxidized into Z + A, resulting in a higher ratio $\frac{Z+A}{V+A+Z}$. During times of limited light energy, the opposite occurs and Z +A is epoxidized into V (*see Fig 1*). On the other hand, over longer, seasonal time scales sustained forms of NPQ work to downregulate photosynthesis in response to prolonged environmental stress. Sustained NPQ is associated with changing pigment pools, overnight retention of zeaxanthin, as well as photoinhibition and other xanthophyll-independent mechanisms (Verhoeven 2014).

The deepoxidation of the xanthophyll cycle and formation of Z+A reduces reflectance at wavelength 531 (see *Fig 1*), forming the theory behind the remotely sensed Photochemical

Reflectance Index (PRI) (Gamon et al. 1997). PRI measures the reflectance in the blue (chlorophyll and carotenoid absorption) at 531nm, normalized to reflectance in the red at 570nm (chlorophyll only absorption) (Gamon et al. 1992). Therefore, in contrast to indices which approximate fAPAR, PRI is theoretically a proxy of LUE.

The amount of APAR a plant can use safely in photosynthesis depends on the physiological state of the plant (Papageorgiou and Govindjee 2014), and the presence of any environmental stress that slows C assimilation can cause light energy to be absorbed in excess (*see Fig 1*; Demmig-Adams et al. 2012). For example, under water-limited conditions stomata close and photosynthesis becomes limited by $CO_2$ diffusion, causing photochemical quenching to slow and NPQ to rise (Medrano et al. 2002). In accordance, PRI has been shown to vary with changing environmental conditions across spatiotemporal scales, such as altered nutrient status (Gamon et al. 1997; Magney et al. 2016), water status (Filella et al. 2004; Inoue and Penuelas 2006), and temperature (Dobrowski et al. 2005; Porcar-Castell et al. 2012). As a result, the relationship between PRI and LUE has been thus far ecosystem or site specific, and a universal relationship remains elusive (Goerner et al. 2011).

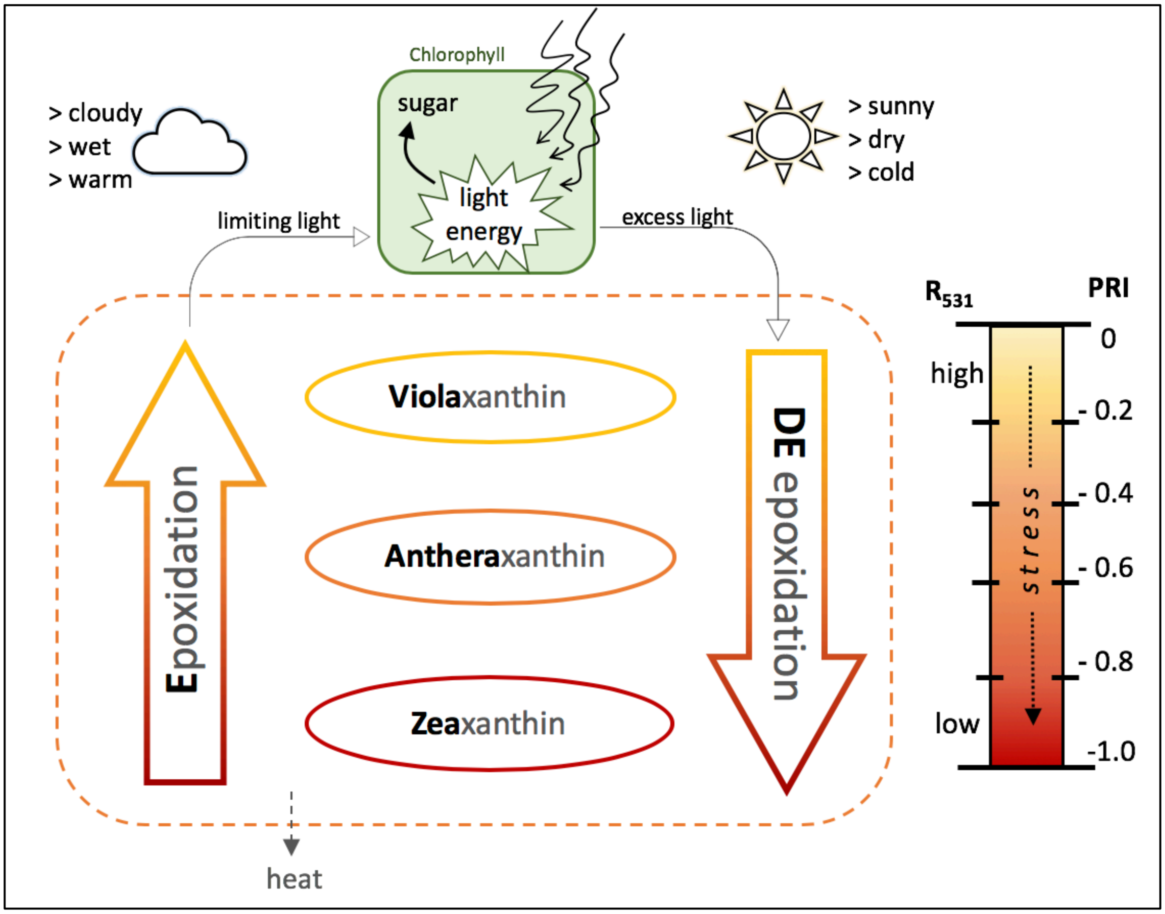

*Fig 1: Conceptual diagram of the xanthophyll cycle and how it relates to PRI. Under excess light, produced by sunny or stressed (dry/cold) conditions, violaxanthin is de-epoxidized into zeaxanthin and* $R_{531}$ *decreases, making PRI more negative. Under limiting light, such as in cloudy or unstressed (wet/warm) conditions, zeaxanthin is epoxidized into violaxanthin and* $R_{531}$ *increases, making PRI less negative. Figure adapted from (Gamon 2015).*

The xanthophyll cycle is therefore related to stress mediated reductions in photosynthesis, operating on a timescale of minutes, and PRI is one of the only pigment-based vegetation indices sensitive to rapid plant physiological responses (Gamon et al. 1992; Penuelas et al. 1995). This is in contrast to other pigment-based indices such as NDVI, which operate mostly on seasonal timescales and were designed based on the pigment and structural dynamics of deciduous and herbaceous ecosystems. We have known for many years that NDVI is a poor indicator of dynamic C fluxes in slow growing evergreen species that persist through prolonged periods of environmental stress (Gamon et al. 1995; Garbulsky et al. 2008; Running and Nemani 1988), but solutions to this challenge have been slow to develop. In addition, even the most advanced remotely sensed products, such as GPP derived from Moderate Resolution Imaging Spectroradiometer (MODIS) product (modGPP), are insensitive to drought induced reductions in forest productivity (Vicca et al. 2016). Therefore, PRI presents new opportunities to study ecosystems on a diurnal time scale, as well as seasonal processes in evergreen systems that are more dynamic than the small annual changes in chlorophyll content. Development of a robust PRI could lead to improvements in the remote sensing of evergreen phenology (Ulsig et al. 2017; Wong and Gamon 2015), as well as drought detection from space (Vicca et al. 2016). Therefore, PRI has the potential to fill a major gap in our ability to distinguish how water availability influences forest productivity and associated C dynamics at broad scales and high temporal resolution.

To aid in this development, systematic PRI acquisition in conjunction with EC flux and leaf photosynthesis measurements are needed across diverse ecosystems (Gamon et al. 2010). One of the greatest barriers to a complete understanding of the global C cycle is the difficulty in reconciling estimates obtained across different spatiotemporal scales. Unlike gas exchange methods which are restricted to the specific spatial domain for which they were developed, optical data can be sampled at the leaf, canopy and ecosystem scales using multiple handheld, tower-mounted, airborne and satellite sensors that measure reflectance data at different resolutions. Therefore, the growing field of proximal remote sensing affords the unique opportunity to bridge leaf, canopy, and ecosystem scales, for a physiological inspection of whole ecosystem dynamics (Gamon 2015). For decades studies have measured PRI using hand held and tower mounted spectrometers, hyperspectral imaging, unmanned aerial platforms, as well as MODIS satellite data (for reviews and metanalyses, see Garbulsky et al. 2011; Zhang et al.

2016). However, the great majority of these studies have been performed in broadleaf, crop, or herbaceous systems, and only a small fraction have analyzed the use of PRI in natural conifer forests or semi-arid ecosystems.

## *1.2 Objectives*

In this study, we measured PRI in conjunction with C and $H_2O$ fluxes in a semi-arid, sub-alpine mixed conifer forest, in order to assess its ability to serve as a proxy for dynamic photoprotection across spatiotemporal scales. The specific objectives of this study were:

1) at the canopy level determine the sensitivity of PRI to a) diurnal and seasonal changes in GPP in a mature conifer forest with an atypical, bimodal growing season; and b) rapid changes in a high stress, semi-arid environment subject to monsoonal precipitation pulses; and

2) at the leaf level a) determine the sensitivity of PRI to diurnal changes in needle photosynthetic function; and b) confirm the extent to which canopy diurnal patterns reflect leaf physiology.

# 2. PRESENT STUDY

## *2.1 Study Site*

The site is a semi-arid sub-alpine mixed conifer forest in the Coronado National Forest on Mt. Bigelow, north of Tucson, Arizona, and is part of the Santa Catalina-Jemez River Basin

Critical Zone Observatory. The site is at 2573m elevation in an area considered to be topographically complex. The climate is semi-arid: mean annual temperature is 9.4 °C and mean annual precipitation is 750mm, though interannual variability is notably high. Of this, ~50% falls during the North American Monsoon in late summer, when a large portion may become surface runoff. The composition of the site is mature second-growth Douglas Fir (*Pseudotsuga menziesii*), Ponderosa Pine (*Pinus ponderosa*), and Southwestern White Pine (*Pinus strobiformis*), with little to no understory vegetation. The forest exhibits a complex and atypical bimodal pattern of production, with an initial spring peak following snow melt, a dry pre-monsoon mid-season depression (May-June), and a second peak of productivity during the wet monsoon (July-Sept), remaining active through fall (*see Appendix B, Fig 8*). Unlike many montane forests which undergo complete winter dormancy, there is evidence that trees remain photosynthetically active during winter months due to mild temperatures and unfrozen soils (J. Knowles, unpublished data). Few other studies have been done in systems which exhibit a bimodal pattern of production, or in conifer forests that retain winter photosynthetic capacity.

## 2.2 Summary of Methods

*2.2.1 Canopy Scale:* We combined tower-mounted canopy spectral measurements with eddy covariance flux and sap flow methods to determine the sensitivity of PRI to seasonal changes in GPP and the ecohydrological dynamics of a high stress environment. An eddy covariance flux tower was used to measure ecosystem-scale $CO_2$, water vapor, and energy fluxes at 30-minute temporal resolution. The EC flux method measures net ecosystem exchange (NEE), which was partitioned into its components GPP and ecosystem respiration (Lasslop et al. 2010), and LUE was calculated as GPP per unit photosynthetic photon flux density (PPFD). The flux footprint was seasonally consistent, and 80% of flux originated from within approximately 750 horizontal meters of the tower (J. Knowles, unpublished data; Kljun et al. 2015). In addition, sap flow was measured every 30 minutes using the thermal dissipation probe method (Granier 1985; Granier 1987) on 5 individual trees. Briefly, this method measures the temperature difference between an upper heated probe and a lower reference probe implanted in the sapwood of the tree, and as sap flow increases due to transpiration, the temperature difference between the two probes is reduced. Therefore, sap flow serves as an estimate of whole tree transpiration. In addition, soil volumetric water content (VWC) was measured continuously using three sets of water content reflectometers buried at 5cm and 15cm depth. We installed a Spectral Reflectance Sensor (SRS, METER Group, Inc., Pullman, WA, USA) at 24m height, roughly 12m above the canopy to collect PRI data every 10 minutes. The field of view (FOV) of the sensor is ~50m$^2$, and slightly biases eastern facing needles of *P. ponderosa* and *P. strobiformis*. We restrict canopy scale analysis to a) the monsoon season in July-September, b) times when sun-sensor angle <40° following Mottus et al. (2015), and c) data where PPFD >1000μmol m$^{-2}$s$^{-1}$. Data were then summarized into a single daily value by taking the morning average from 10:00 -12:00. These restrictions were to maximize sunlit canopy surface viewed by the sensor and minimize effects of changing solar geometry.

*2.2.2. Leaf Scale:* Leaf gas exchange with simultaneous chlorophyll fluorescence and spot hyperspectral measurements were taken to determine the sensitivity of PRI to diurnal changes in needle function, and confirm the extent to which canopy diurnal patterns reflect leaf diurnal physiology. Leaf level measurements were taken on September 13-14 for one *P. ponderosa* and one *P. strobiformis* mature tree on attached top of canopy needles (13m height) using a canopy access crane. We measured 4 sunlit branches on each tree every hour from 9:00-

16:00. These data were averaged to give hourly data for each species, however some data were excluded due to cloudiness. Gas exchange with simultaneous pulse amplitude modulated (PAM) fluorescence was accomplished using the Li-6800 Portable Photosynthesis System infrared gas analyzer (LICOR Inc., Lincoln, NE, USA). Gas exchange measurements are the most established and commonly used field technique in plant ecophysiology and these methods have a high degree of confidence (Long and Bernacchi 2003). Point measurements were taken to obtain net photosynthesis ($A_{net}$), stomatal conductance (gsw), and LUE. PAM fluorometry measured quantum yield of photosystem II (ΦPSII), NPQ, and maximal photochemical efficiency of ΦPSII (Fv/Fm) according to Bilger and Bjorkman (1990) and Genty et al. (1989). To obtain NPQ and Fv/Fm, dark-adapted fluorescence measurements were also taken at pre-dawn for a minimum of 8 samples per branch. In addition, leaf level hyperspectral reflectance measurements were taken with an ASD FieldSpec3 (ASD Inc., Boulder, CO, USA) spectroradiometer with an artificial light source, calibration surface and a leaf clip. Within ten seconds of measurement, needles were detached and preserved in liquid nitrogen for future biochemical pigment analysis.

## *2.3 Summary of Results*

*2.3.1 Inconsistent PRI-GPP seasonal relationships:* At the canopy scale we found that the relationship between PRI and GPP changed over the course of the monsoon season, shifting from a significant negative relationship in July and August ($R^2$=.62), to a significant positive relationship in September ($R^2$=.48). These results agree with the few other studies that have been conducted under a monsoon climate, which also reported inconsistent and weaker relationships with estimates of productivity (Nakaji et al. 2014; Nakaji et al. 2006; Zhang et al. 2015). The breakdown of the PRI-GPP relationship in July-August could be due to a) high frequency rain events b) changing carotenoid/chlorophyll pigment pools following the transition out of pre-monsoon sustained suppression, or c) a footprint mismatch between EC flux and optical data.

2.3.2 *Seasonal PRI responds to ecohydrological dynamics:* Daily average PRI was significantly, albeit weakly, correlated with VWC ($p<0.05$, $R^2=0.17$), as well as with $T_{air}$ ($p<0.05$, $R^2=0.10$). Multiple linear regression (MLR) with VWC and $T_{air}$ show that PRI is responding to dynamic water and energy limitations of this system ($R^2=.41$, 5-fold cross-validated $R^2=.35$). These results agree with long-term EC records which indicate that this forest can be both water and/or energy limited depending on prevailing conditions (unpublished data, J. Knowles). The results of the MLR are strengthened by a sap flow analysis where we showed that PRI was significantly related to transpiration from late July through mid-September ($R^2=.55$). In addition, PRI performed more strongly than GPP at tracking the three-month time course of sap flow. Because the SRS sensor measured the full or partial canopy of the same 5 trees used to measure sap flow, the spatial scales of PRI and sap flow measurements were nearly identical, which we believe contributes to their close correlation. This is the first study to our knowledge to report a relationship between PRI and sap flow in a natural mature forest, the first to do so using canopy PRI, and the first to show this relationship on a seasonal time scale with continuous, daily resolution. These sap flow results, combined with the MLR relationship to VWC and $T_{air}$, suggest that on a seasonal scale PRI is an effective indicator of photoprotective response to ecohydrological constraints.

2.3.3 *Suppressed Diurnal PRI response:* Rather than parallel irradiance conditions of the diurnal cycle, we found that PRI remained constant throughout the day, both at the canopy and leaf scales. We hypothesize that in this high light, high temperature environment, retention of zeaxanthin through day and night keep top of canopy needles poised for flexible engagement. This hypothesis is supported by very high NPQ and very low ΦPSII values, but with no concurrent reductions in Fv/Fm. Agreement between leaf-level measurements, which are not subject to structural and geometrical effects, and canopy-level measurements that integrate over leaf heterogeneity, strengthen our confidence that the demonstrated lack of PRI diurnal response is in fact rooted in physiology.

## *2.4 Conclusions*

Remotely sensed PRI holds potential to fill a major gap in our ability to distinguish how water availability influences productivity and associated C dynamics, particularly in evergreen systems. However, spectral data in conjunction with C and $H_2O$ flux measurements are needed to provide a functional examination of PRI as a proxy for dynamic photoprotection. At the canopy scale we found that the relationship between PRI and GPP changed over the course of the monsoon season. Despite a seasonal decoupling, we report for the first time a relationship between PRI and sap flow in a natural forest, and contribute evidence that PRI is sensitive to ecohydrological dynamics. Because photosynthetic function is linked more directly to stomatal conductance than to foliar water status (Medrano et al. 2002), and because reductions in leaf water content occur only after advanced stages of drought, PRI represents an improved capacity over foliar water content indices to serve as an early indicator of water stress (Inoue and Penuelas 2006). Remote sensing has proven to be a powerful tool for monitoring past and ongoing ecosystem disturbances such as drought induced forest mortality, however to harness the full potential of these technologies, progress should be made in our ability to predict when ecosystems will be vulnerable to future degradation prior to visible manifestations (Smith et al.

2014). PRI has potential as an a priori approach for predicting plant response to future changes in hydroclimate.

Characterization of diurnal PRI is needed if snapshot satellite data can ever serve as a robust representation of photosynthetic processes (Sims et al. 2005), yet at present, information of diurnal PRI is limited in natural systems, particularly in mature conifer forests (Gamon and Bond 2013; Mottus et al. 2018). This is the first study to analyze diurnal needle PRI and its relationship with combined gas exchange, fluorescence, and NPQ parameters in top of canopy needles of a montane conifer forest. We found that an instantaneous measurement of canopy PRI would not be representative of instantaneous photosynthesis in this system. Suppressed diurnal PRI dynamics in conifers may reflect a long-term retention of zeaxanthin or upregulation of alternative photoprotective mechanisms when canopies experience prolonged stress.

## *2.5 Future Directions*

Overall, we found that the ability of PRI to serve as a proxy for seasonal and diurnal environmental stress response in a semi-arid conifer forest was inconsistent through time. Therefore, more work is needed to probe into the mechanistic drivers of these results. We suggest that to investigate further, this analysis should be repeated multiple times throughout the season: during active winter periods, spring peak, pre-monsoon shutdown, and again during senescence, paying particular attention to the transition between pre-monsoon drought and monsoon re-wetting. Seasonally iterated diurnal analysis should be paired with biochemical pigment characterization to help discern if PRI is representing xanthophyll cycle activity versus larger pigment pool changes. We hypothesize that because the influence of precipitation pulses in semi-arid ecosystems causes functional processes to decouple over relatively short time scales

(Huxman et al. 2004), temporal phase misalignments may complicate the relationships between PRI, transpiration, GPP, and pigment composition in this semi-arid forest (Ruehr et al. 2012) as compared to more mesic sites.

Though a number of studies have explored the extent to which seasonal PRI is mediated by water stress (He et al. 2016; Magney et al. 2016; Moreno et al. 2012; Nestola et al. 2018; Penuelas et al. 1998; Ripullone et al. 2011; Soudani et al. 2014; Zhang et al. 2017), its presence seems to complicate seasonal PRI-LUE relationships in ways that are not yet understood. While some studies report that PRI is more sensitive to LUE under moderately stressed conditions (Zhang et al. 2015), research also suggests that the sensitivity of PRI to atmospheric water demand has a threshold (Zhang et al. 2017), and the relationship between PRI and LUE has been observed to break down during severe water stress (Guarini et al. 2014; Sims et al. 2006; Tsonev et al. 2014). This suggests that while PRI is related to stress mediated reductions in LUE, it becomes less informative after a threshold in which photosynthesis becomes increasingly limited by metabolic factors causing xanthophyll retention of Z+A, and the use of additional zeaxanthin-independent enhancements of NPQ. Little work has been done to explore the extent to which these processes effect the seasonal PRI relationship to LUE or GPP. Extending our analysis into the pre-monsoon season will aid in understanding how PRI responds to severe, prolonged drought. The tendency for PRI to break down under severe water stress will be important to understand moving into the future as periods of prolonged drought are expected to increase across vast areas.

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# APPENDIX A

## PHOTOCHEMICAL REFLECTANCE INDEX (PRI) IS SENSITIVE TO THE ECOHYDROLOGY OF A SEMI-ARID MIXED CONIFER FOREST.

*To be submitted to Remote Sensing of Environment*

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# ABSTRACT

A lack of accurate, reliable data on coupled carbon and water fluxes for Earth's expansive ecosystems remains a major barrier to a complete understanding of the terrestrial carbon cycle. The remotely sensed Photochemical Reflectance Index (PRI) measures deepoxidation of the xanthophyll cycle at wavelength 531nm and is one of the few pigment-based vegetation indices sensitive to rapid plant physiological responses. PRI presents new opportunities to study ecosystems on a diurnal time scale, as well as seasonal processes in evergreen systems where complex vegetation dynamics are not reflected by small annual changes in chlorophyll content or leaf structure. However, systematic PRI acquisition in conjunction with leaf and ecosystem flux measurements are needed in natural, diverse ecosystems. The growing field of proximal remote sensing affords the opportunity to bridge leaf, canopy and ecosystem scales, for a physiological inspection of whole ecosystem dynamics. The Southwest U.S. provides a natural setting for examining the influence of environmental drivers on the productivity of drought-sensitive forests, as well as for evaluating our ability to track these relationships using optical methods. We studied PRI in a semi-arid, sub-alpine mixed conifer forest, in order to assess its ability to serve as a proxy for dynamic photoprotection. We combined canopy spectral measurements with eddy covariance flux and sap flow methods to determine the sensitivity of PRI to seasonal changes in gross primary productivity (GPP) and the ecohydrological variability of a high stress environment. In addition, we combined top-of-canopy leaf-level gas exchange, chlorophyll fluorescence, and hyperspectral measurements to determine the sensitivity of PRI to diurnal changes in needle photosynthetic function, and confirm the extent to which canopy diurnal patterns reflect leaf physiology. At the canopy scale we found that the relationship between PRI and GPP was inconsistent over the course of the monsoon season, shifting from a negative relationship in July and August ($R^2$=.62), to a positive relationship in September ($R^2$=.48). Multiple linear regression with soil moisture and air temperature showed that PRI responded to dynamic water and energy limitations of this system ($R^2$=.41). We report for the first time a relationship between seasonal PRI and sap flow in a natural forest ($R^2$=.55). These results suggest that on a seasonal scale PRI is an effective indicator of photosynthetic response to ecohydrological constraints. On a diurnal scale we found that PRI remained constant throughout the day at both leaf and canopy scales, and we suggest that saturated light conditions drive retention of xanthophylls in a de-epoxidized state. We contribute evidence that remotely sensed PRI has potential to fill a major gap in our ability to distinguish how water availability influences forest productivity and associated carbon dynamics.

**Keywords**: conifer, semi-arid, eddy covariance flux, sap flow, gas exchange, chlorophyll fluorescence, non-photochemical quenching (NPQ), xanthophyll cycle, photochemical reflectance index (PRI), seasonal, diurnal

# 1. INTRODUCTION

Accurate modeling of the global carbon (C) cycle is critical for understanding and predicting a wide range of feedbacks between climate and the terrestrial biosphere. Estimating terrestrial gross primary productivity (GPP) is a major goal of Earth systems science (Beer et al. 2010; Makela et al. 2008; Piao et al. 2013; Smith et al. 2016), yet major uncertainties persist and it remains an ongoing challenge for ecologists to provide high-quality data and reduce errors in uncontrolled field settings (Ryu et al. 2019). A complete understanding of the terrestrial C cycle depends on our ability to understand seasonal changes in photosynthetic function, and how this is correlated with environmental constraints across time. Net fluxes of C and water can be quantified at the ecosystem level using eddy covariance (EC) flux towers (Baldocchi 2008), and at the leaf level using chamber enclosure systems (Long and Bernacchi 2003). While field methods at the leaf and canopy scale obtain irreplaceable mechanistic information, they are expensive, time intensive, and reinforce a problematic data bias towards locations with ease of access (Schimel et al. 2015). Thus, for decades, remote sensing studies have provided estimates of terrestrial productivity from ecosystem to global scales (Field et al. 1995; Jung et al. 2011; Prince and Goward 1995; Running et al. 2004; Schimel et al. 2015), providing critical input for Earth system models.

However, Biederman et al. (2017) showed that models based on MODIS satellite observations largely fail to capture the high degree of C and $H_2O$ flux temporal variability in semi-arid ecosystems, which are highly sensitive to precipitation inputs and climate anomalies (Scott et al. 2015). Therefore, improving the capability of remote sensing to monitor C flux response to hydrologic variability is needed. In particular, this is important for monitoring and predicting changes in montane forests across the western U.S., which account for the majority of carbon dioxide ($CO_2$) uptake in the region (Schimel et al. 2002). These forests are already sensitive to changing water availability (Monson et al. 2002) and are projected to experience severe increases in drought under future climate scenarios (Williams et al. 2013). Yet, we have an incomplete understanding of forest decline due to drought (Allen et al. 2010), and our ability to model tree-water relations is limited by a lack of robust methodology for measuring coupled C and water fluxes on large scales. The ongoing heat-driven drought makes the Southwest U.S. a natural setting for examining the influence of environmental drivers on the productivity of drought-sensitive forests (Seager et al. 2007; Udall and Overpeck 2017), as well as evaluating our ability to track these relationships using optical methods.

The light use efficiency (LUE) model (*equation 1*), originally developed by John Monteith (Monteith 1972, 1977), has been the paradigm in remote sensing to evaluate GPP on ecosystem to global scales (Field et al. 1995; Hilker et al. 2008b) and is expressed as:

$$\begin{aligned} GPP &= APAR * LUE \\ APAR &= fAPAR * PAR \end{aligned} \qquad \text{Equation 1}$$

Where LUE is the light use efficiency term, and APAR is the absorbed photosynthetically active radiation (PAR): equal to the total amount of PAR times the fraction absorbed by the canopy (fAPAR). For better or for worse, this simple equation based on first principles attempts to encompass a complex tangle of biological processes. While fAPAR can be seen as a biophysical term that represents long-term variability in vegetation structure and composition, LUE is a functional term that reflects short-term variability in physiological response to less-than-ideal environmental conditions (Porcar-Castell et al. 2014). Typically, indices based on leaf pigment and structure reflectance properties such as the normalized difference vegetation index (NDVI) have been used to estimate changes in the fAPAR term (Goward and Huemmrich 1992; Myneni et al. 1997; Myneni and Williams 1994; Sellers 1985), while adjusting for LUE based on parameterized responses to coarse meteorological data (e.g. VPD and temperature) and assuming LUE response to these drivers remains constant (Running et al. 2004). However, it has been shown that LUE is far from constant (Gamon et al. 1992; Sinclair and Muchow 1999; He et al. 2016) – it varies over time and space, and allowing LUE to vary improves estimation of gross ecosystem production (Rossini et al. 2010).

LUE is controlled by a diverse set of photoprotective processes working in concert, and the biology of these processes and their interactions are not fully understood even at the thylakoid level. When a plant absorbs radiant energy in excess of what it can use to drive electron transport, it must dissipate energy that would otherwise cause photo-oxidative damage (Barber and Andersson 1992; Demmig-Adams and Adams 2000). This energy dissipation occurs through various mechanisms, but the primary pathway is through non-photochemical quenching (NPQ) via xanthophyll pigments (Demmig-Adams and Adams 1992, 1996; Muller et al. 2001). Xanthophyll pigments regulate flexible NPQ processes, which operate on diurnal time scales and reset each night (Demmig-Adams and Adams 2006; Muller et al. 2001; Porcar-Castell 2011). Three forms – violaxanthin (V), antheraxanthin (A), and zeaxanthin (Z)—are interconverted through enzymatic reactions involving an epoxy group. During times of excess light energy, V is de-epoxidized into Z + A, resulting in a higher ratio $\frac{Z+A}{V+A+Z}$. During times of limiting light, the opposite occurs and Z +A is epoxidized into V. On the other hand, over longer, seasonal time scales sustained forms of NPQ work to downregulate photosynthesis in response to prolonged environmental stress. Sustained NPQ is associated with changing pigment pools, overnight retention of zeaxanthin, as well as photoinhibition and other xanthophyll-independent mechanisms (Verhoeven 2014).

The deepoxidation of the xanthophyll cycle and formation of Z+A reduces reflectance at wavelength 531, forming the theory behind the remotely sensed Photochemical Reflectance Index (PRI) (Gamon et al. 1997). PRI measures reflectance in the blue (chlorophyll and carotenoid absorption) at 531nm, normalized to reflectance in the red at 570nm (chlorophyll only absorption) (Gamon et al. 1992). Therefore, in contrast to indices which approximate fAPAR, PRI represents an estimate of LUE.

The amount of APAR a plant can use safely in photosynthesis depends on the physiological state of the plant (Papageorgiou and Govindjee 2014), and the presence of any environmental stress that slows C assimilation can cause light energy to be absorbed in excess (Demmig-Adams et al. 2012). The xanthophyll cycle is therefore related to stress mediated reductions in photosynthesis, operating on a timescale of minutes, and PRI is one of the only pigment-based vegetation indices sensitive to rapid plant physiological responses (Gamon et al. 1992; Penuelas et al. 1995). In accordance, PRI has been shown to vary with changing environmental conditions, such as altered nutrient status (Gamon et al. 1997; Magney et al. 2016), water stress (Filella et al. 2004; Inoue and Penuelas 2006), and temperature (Dobrowski et al. 2005; Porcar-Castell et al. 2012). As a result, the relationship between PRI and LUE has been thus far ecosystem or site specific, and a universal relationship remains elusive (Goerner et al. 2011).

To aid in its development, systematic PRI acquisition in conjunction with EC flux and leaf photosynthesis measurements are needed (Gamon et al. 2010). One of the greatest barriers to a complete understanding of the C cycle is the difficulty in reconciling estimates obtained across different spatiotemporal scales. Therefore, the growing field of proximal remote sensing affords the unique opportunity to bridge leaf, canopy, and ecosystem scales, for a physiological inspection of whole ecosystem dynamics (Gamon 2015; Shiklomanov et al. 2019). For decades studies have measured PRI across spatiotemporal scales using hand held and tower mounted spectrometers, hyperspectral imaging, unmanned aerial platforms, as well as MODIS satellite data (for reviews and metanalyses, see Garbulsky et al. 2011; Zhang et al. 2016). However, the great majority of these studies have been performed in broadleaf, crop, or herbaceous systems, and only a small fraction have analyzed the use of PRI in natural conifer forests or semi-arid ecosystems. In this study, we measured the PRI in conjunction with C and $H_2O$ fluxes in a semi-arid, sub-alpine mixed conifer forest, in order assess its ability to serve as a proxy for dynamic photoprotection. At the canopy scale, our specific objectives were to: 1a) determine the sensitivity of PRI to diurnal and seasonal changes in GPP in a mature conifer forest with an atypical growing season; and 1b) determine the sensitivity of PRI to climatic variability in a high stress, semi-arid environment subject to monsoonal precipitation pulses. At the leaf scale, our objectives were to 2a) determine the sensitivity of PRI to diurnal changes in needle function; and 2b) confirm the extent to which canopy diurnal patterns reflect leaf physiology.

# 2. METHODS

## *2.1 Study Site*

The site is a semi-arid sub-alpine mixed conifer forest in the Coronado National Forest on Mt. Bigelow, north of Tucson, Arizona, and is part of the Santa Catalina-Jemez River Basin Critical Zone Observatory. The site is at 2573m elevation in an area that is considered topographically complex. The climate is semi-arid: mean annual temperature is 9.4 °C and mean annual precipitation is 750mm, though interannual variability is notably high. Of this, ~50% falls during the North American Monsoon in late summer, when a large portion may become surface runoff. The composition of the site is mature second-growth Douglas Fir (*Pseudotsuga menziesii*), Ponderosa Pine (*Pinus ponderosa*), and Southwestern White Pine (*Pinus strobiformis*), with little to no understory vegetation. The forest exhibits a complex and atypical bimodal pattern of production, with an initial spring peak following snow melt, a dry pre-monsoon mid-season depression (May-June), and a second peak of productivity during the wet monsoon (July-Sept), remaining active through fall (*Appendix B, Fig 8*). Unlike many montane forests which undergo complete winter dormancy, there is evidence that trees remain photosynthetically active during winter months (J. Knowles, unpublished data) due to mild temperatures and unfrozen soils.

### *2.2 Eddy Covariance Fluxes*

An EC flux tower was used to measure ecosystem-scale $CO_2$, water vapor, and energy fluxes. The EC flux tower has been in continuous operation since 2009 and is equipped with an open-path infrared gas analyzer (IRGA; LI-7500, Li-COR, Lincoln, NE, USA) and a three-dimensional sonic anemometer (CSAT 3, Campbell Scientific, Logan, UT, USA) at 29.8m height oriented to 290°. Facing south is a PAR sensor (LI-190, LI-COR, Lincoln, NE, USA) at 25m height, and an air temperature ($T_{air}$) and relative humidity sensor (HMP45C, Vaisala, Helsinki, Finland) at 1.5m height. Data were sampled at 10 Hz (sonic anemometer and IRGA) or five minutes (all other sensors) and recorded and averaged to 30-min values by a datalogger (CR5000, Campbell Scientific, Logan, UT, USA); manual data collection was performed approximately bi-weekly. All tower operations were powered by solar panels. Standard protocols were used to filter the turbulent flux data for accuracy and quality (Lee et al. 2004). The net ecosystem exchange of $CO_2$ (NEE) was further partitioned into GPP and ecosystem respiration using a light response curve methodology (Lasslop et al. 2010). Data were gap-filled using a look up table approach (Falge et al. 2001). The statistical flux footprint was seasonally consistent and 80% of flux originated from within approximately 750 horizontal meters of the tower (J. Knowles, unpublished data; Kljun et al. 2015). LUE was calculated as GPP per unit photosynthetic photon flux density (PPFD), due to a lack of robust estimate of APAR. The use of PAR when APAR is unavailable can have an impact on seasonal changes in LUE (Gitelson and Gamon 2015), however, changes in fAPAR over the course of the study are minimal according to NDVI (see *Appendix B, Fig 9*).

### *2.3 Ecohydrology*

Sap flow was measured using the thermal dissipation probe method (Granier 1985; Granier 1987) logged at 30 min resolution. Briefly, this method measures the temperature difference between an upper heated probe and a lower reference probe (TDP-30, Dynamax Inc., Houston, TX, USA) implanted in the sapwood of the tree approximately 40mm apart. As sap flow increases due to transpiration, the temperature difference between two points is reduced. Sap flow velocity (cm $hr^{-1}$) was calculated according to equation:

$$\begin{gathered} V_s = 0.0119K^{1.231} \\ K = (dTM - dT)/dT \end{gathered} \qquad \text{Equation 2}$$

Where dT is the difference in temperature (°C) between the two needles, and dTM is dT when there is no sap flow. Sap flow was measured on the north and south sides of three *P. strobiformis* and two *P. ponderosa* individuals. In addition, soil volumetric water content (VWC) was measured continuously using three sets of water content reflectometers (CS 616; Campbell Scientific, Logan, UT, USA) buried at 5cm and 15cm depth beneath the soil surface on the east, north, and south of the tower. Daytime measurements from these six probes were averaged to obtain a single daily VWC value.

### *2.4 Canopy Spectral Measurements*

On July 4, 2018, a Spectral Reflectance Sensor (SRS, METER Group, Inc., Pullman, WA, USA) was installed, collecting 10-min resolution PRI reflectance. A few studies have demonstrated successful use of these or similar autonomous sensors (Castro and Sanchez-Azofeifa 2018; Eitel et al. 2019; Gamon et al. 2015; Garrity et al. 2010; Magney et al. 2016; van Leeuwen et al. 2015). The PRI sensors use photodiodes with narrow bandpass filters centered at wavelengths 532 and 570nm with 10 nm full width half maximum (FWHM) bandwidths. It uses a hemispherical upward-looking sensor, and a field stop downward-looking sensor to measure incoming and upwelling radiation (W $m^{-2}$ $sr^{-1}$ $nm^{-1}$), respectively. The upward looking sensor contains a cosine diffuser to provide continuous 180° irradiance measurements that are used to normalize downward looking spectral radiance. PRI is calculated as:

$$PRI = \frac{\rho_{532} - \rho_{570}}{\rho_{532} + \rho_{570}} \qquad \text{Equation 3}$$

Where $\rho_{532}$ is the spectral reflectance value at center wavelength of 532 nm and $\rho_{570}$ is the spectral reflectance value at center wavelength of 570 nm. Downward looking sensor interference filters restrict the field of view (FOV) to 36°. The sensor sits at 24m height and is roughly 12m above the top of the canopy titled off-nadir at an angle of 20°, making its footprint coverage ~50$m^2$. The SRS sensor points west, therefore biasing eastern facing needles in its measurement. After 3-4 months of measurement, the sensor glue has been reported to degrade from UV exposure (personal correspondence), therefore we limit our analysis to the monsoon season of July, August, and September (DOY 186-279, *Appendix B, Fig 8*). In addition, we restrict our analysis to data points where sun-sensor angles <40° following Mottus et al. (2015), who found geometry effects on canopy PRI was small for solar zenith angles (SZA) within this range. Within the FOV are full or partial canopies of five trees (three *P. ponderosa* and two *P. strobiformis*) four of which were equipped with sap flow sensors.

For seasonal analysis, data is summarized into one daily value by taking the morning average (10:00 -12:00) for all data when PPFD>1000 µmol $m^{-2}s^{-1}$. Because our sensor biases eastern facing needles, this should represent conditions with the highest sun:shade illumination fraction. This minimizes the effects of canopy shading caused by sun angle, which can strongly influence the relationship between canopy PRI and LUE (Hall et al. 2011; Hall et al. 2008; Hilker et al. 2008a; Hilker et al. 2010). The selection of this time frame follows previous studies which have observed that the highest correlations between PRI and LUE occur under clear sky conditions and for sunlit canopy surface (Gamon et al. 1997; Hall et al. 2008; Soudani et al. 2014), and that on sunny summer days, sun leaves are not affected by SZA (Middleton et al. 2009). We note that with this approach, the proportion of sunlit needles observed by the sensor may not be representative of the proportion within the entire EC flux footprint. However, in such a high light environment, we assume that a large portion of the canopy is light saturated throughout much of the day.

### *2.5 Leaf campaign*

Leaf level measurements were taken on September 13-14 for one *P. ponderosa* and one *P. strobiformis* mature tree on attached top of canopy needles (13m height) using a canopy access crane. The measured trees were not directly under the SRS sensor so as not to disturb to signal; however, they were adjacent and of the same size, age class, and topographic position.

We measured four branches on each tree every hour from 9:00-16:00. Two sunlit fascicles were measured for simultaneous gas exchange and fluorescence, representing six needles for *P. ponderosa* and ten needles for *P. strobiformis*. Immediately after, those same needles, plus two more fascicles, were measured with a spectroradiometer. When measuring under intermittent cloudiness, measurements were aborted if the needles were not exposed to sunlight immediately prior to both gas exchange and spectral measurements.

### *2.5.1 Combined gas exchange and fluorescence*

Gas exchange with simultaneous fluorescence measurements were taken using the Li-6800 Portable Photosynthesis System infrared gas analyzer (LICOR Inc., Lincoln, NE, USA). Gas exchange measurements are the most established and commonly used field technique in plant ecophysiology and these methods have a high degree of confidence (Long and Bernacchi 2003). Spot measurements were taken to obtain net photosynthesis ($A_{net}$), stomatal conductance (gsw), and LUE. For each round of branch measurements, $T_{air}$ and PAR were characterized, and internal chamber conditions set to match the ambient environment. We performed leaf area analysis on ten samples of each species to get an average leaf area within the chamber ($2.24 cm^2 \pm 0.16 cm^2$ and $2.22 \pm 0.22 cm^2$ for *P. ponderosa* and *P. strobiformis*, respectively) assuming each sample clamped the same approximate amount of leaf area.

Pulse amplitude modulated (PAM) fluorescence was used to obtain the quantum yield of photosystem II (ΦPSII), NPQ, and maximal photochemical efficiency of photosystem II (Fv/Fm) according to (Bilger and Bjorkman 1990; Genty et al. 1989):

$$\Phi\text{PSII} = \frac{F_m' - F_s}{F_m{'}} \qquad NPQ = \frac{F_m - F_m{'}}{F_m{'}} \qquad \frac{Fv}{Fm} = \frac{F_m - F_o}{F_m}$$

Where $F_m$ and $F_o$ are the maximal and minimal fluorescence in a dark-adapted leaf, respectively, $F_m$' is the maximal fluorescence in a light adapted leaf, and Fs is steady state fluorescence. We used the multiphase flash method to obtain greater accuracy in $F_m$' acquisition compared to typical rectangular flash methods (Loriaux et al. 2013). To obtain dark adapted parameters, measurements were taken at pre-dawn for a minimum of eight samples per branch to obtain branch averaged $F_o$ and $F_m$. Average coefficient of variation for each branch was 0.126 and 0.136 for $F_o$ and $F_m$, respectively.

### *2.5.2 Leaf hyperspectral*

In addition, leaf level hyperspectral reflectance measurements were taken with an ASD FieldSpec3 (ASD Inc., Boulder, CO, USA) spectroradiometer with plant probe. The FieldSpec has a spectral range from 350-2500nm with spectral resolution 3nm FWHM and sampling interval 1.4nm in the visible range. The plant probe has a low intensity light source for non-destructive data collection. Prior to each measurement, a white reflectance reference was taken using a calibrated reference standard. Needles were arranged, as best as possible, in a single plane to minimize gaps without being overlapping. After clamping onto the needles and turning on the light source, 2-3 spectra were taken within a few seconds to prevent jumps in PRI due to an altered light condition (Mottus et al. 2017).

## 3. RESULTS

### *3.1 Seasonal PRI versus GPP*

Pooled over the course of the entire study period, PRI and GPP were not statistically related ($p>0.05$, regression not shown). However, we did find a relationship that is inconsistent through time (*See Fig 2b*). There was a significant negative relationship between PRI and GPP in July and August ($R^2$=.62, $p<0.05$, *Fig 2c*), and a significant positive relationship in September ($R^2$=.48, $p<0.05$, *Fig2d*). The seasonal course of LUE was very similar to GPP (*Fig 2b*), and again, PRI was significantly negatively related to LUE in July and August ($p<0.05$, $R^2$=.52), and positively in September ($p<0.05$, $R^2$=.53). As mentioned previously, sunny data from 10:00-12:00 was averaged to summarize each day into a single value. The average standard deviation for each daily PRI data point was ±0.112, however some days displayed a much higher degree of variation in PRI (*see Appendix B, Fig 10a*). Changes in the degree of intra-morning PRI variation over the course of the season are shown in *Appendix B, Fig 10d.* This study period covered a three-month time span from July-September characterized by monsoon convective storms. Hydrologic dynamics showed that July and August were marked by higher frequency storms and more variable atmospheric demand compared to September (*see Fig 2a*). The sudden peak in GPP around August 8 is difficult to explain. There were no sudden changes in the system that would lead us to expect a spike in GPP, therefore this peak may be a modeling artifact resulting from NEE partitioning. Nonetheless, it is curious that this GPP spike corresponds precisely in time with an equally dramatic drop in PRI.

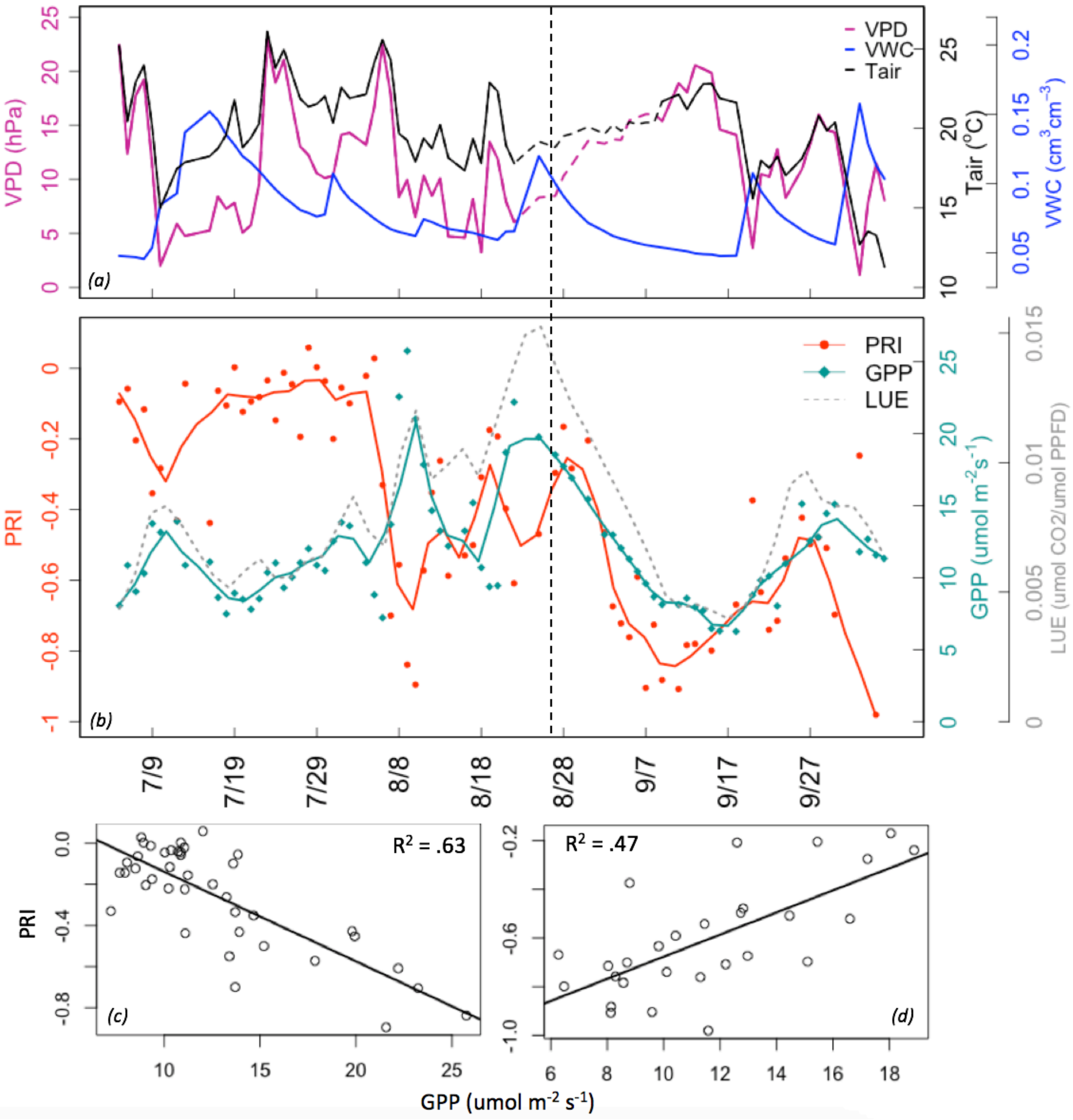


*Fig 2: a) Three-month seasonal time course of VPD (hPa), VWC (cm$^3$cm$^{-3}$), and $T_{air}$ (°C) showing greater hydrologic variability in July and August compared to September; b) seasonal PRI and GPP (μmol $CO_2$ m$^{-2}$ s$^{-1}$), with LUE (μmol $CO_2$/μmol PPFD) shown to demonstrate similarity to GPP. Smoothed seasonal trend lines were created using a 1st order polynomial symmetrical Gaussian function. Dotted trend line segments indicate data that was gap filled. Dividing the data at the dotted line around the end of August, PRI and GPP show c) a significant negative relationship ($R^2$=.63 $p<0.05$) in July and August, and d) a significant positive relationship ($R^2$=.47, $p<0.05$) through September.*

*3.2 Seasonal PRI and the dynamic environment:*

PRI clearly parallels a combination of VWC and $T_{air}$ throughout the season (see *Fig 3a*). Daily average PRI was significantly, albeit weakly, correlated with VWC ($p<0.05$, $R^2=0.17$), as well as with $T_{air}$ ($p<0.05$, $R^2=0.10$). Daily PRI was not significantly correlated with vapor pressure deficit (VPD) or PPFD (*see Table 1*). We performed a regression tree analysis (Breiman et al. 1984) using the recursive partitioning package (the R library rpart – Version 4.1-13) on the environmental drivers of PRI: VWC, $T_{air}$, VPD, and PPFD, and found that $T_{air}$ and VWC ranked highest in importance: $T_{air}$, VWC, VPD, and PPFD had a variable importance of 37%, 29%, 27%, and 7%, respectively. Multiple linear regression (MLR) using VWC and $T_{air}$ significantly but weakly predicted PRI ($R^2=0.41$, $p<0.05$; *See Fig 3b,c,d*)—with the equation: $-2.0791 + 6.4036 * VWC + 0.0585 * T_{air}$. We ran a global validation of linear model assumptions (the R library gvlma – Version 1.0.0.3; Pena and Slate 2006), and all assumptions were met. Cross-validation analysis, in which the model was trained with 70% of the data, tested on the remaining 30%, and iterated five-fold, produced an $R^2=0.35$ (*Fig 3b,c*). Adding PPFD into the model showed no improvements (*see Table 1*). The model performed the weakest during mid-September when VWC was at a minimum (*see Fig 3*).

In contrast, regression tree analysis for the environmental drivers of GPP showed that VPD rather than $T_{air}$ ranked highest in importance. VPD, VWC, PPFD, and $T_{air}$ had a variable importance of 28%, 26%, 24%, and 23%, respectively. GPP was less influenced by VWC and was more sensitive to PPFD, as compared to PRI. These results hint that a decoupling between $T_{air}$ and VPD (i.e. when its humid) could produce more divergence in the PRI-GPP relationship. In fact, only looking at times when VPD - $T_{air} > 10$, there was a strong negative relationship between GPP and PRI ($R^2= 0.56$, $p<0.05$, data not shown). This suggests that it is these times that are driving the negative PRI-GPP relationship in July-August. An MLR model predicting GPP with a combination of VWC and VPD was significant ($p<0.05$), but much weaker ($R^2$=.24) than the prediction of PRI (*see Appendix B, Fig 11*). It was somewhat surprising that PRI could be predicted from the physical environment more strongly than GPP. This highlights the fact that PRI is directly tied to the plant response to environmental stress, while plants are adapted to maximize GPP within environmental constraints.

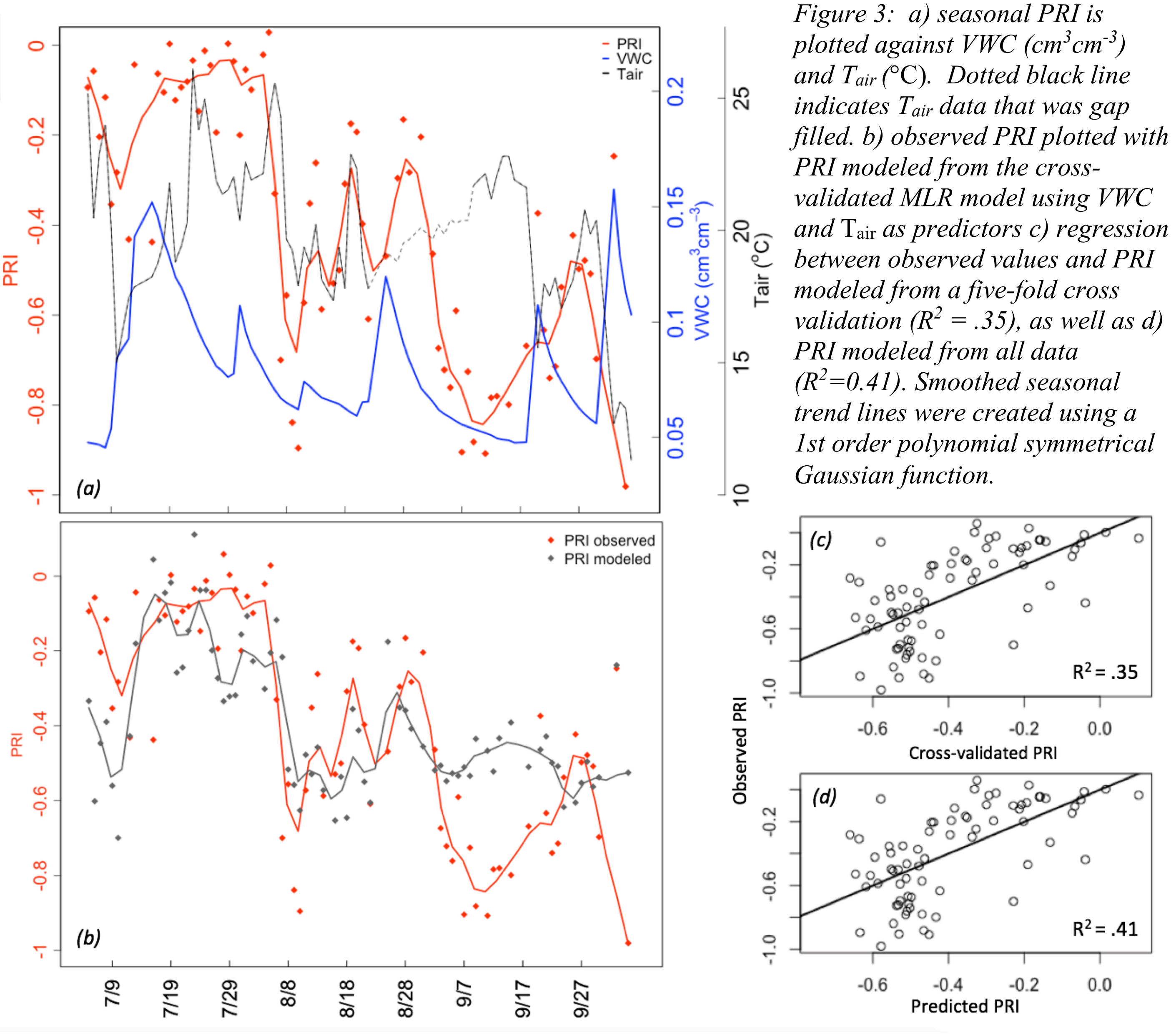


*Figure 3: a) seasonal PRI is plotted against VWC (cm$^3$cm$^{-3}$) and $T_{air}$ (°C). Dotted black line indicates $T_{air}$ data that was gap filled. b) observed PRI plotted with PRI modeled from the cross-validated MLR model using VWC and* $T_{air}$ *as predictors c) regression between observed values and PRI modeled from a five-fold cross validation ($R^2$ = .35), as well as d) PRI modeled from all data ($R^2$=0.41). Smoothed seasonal trend lines were created using a 1st order polynomial symmetrical Gaussian function.*

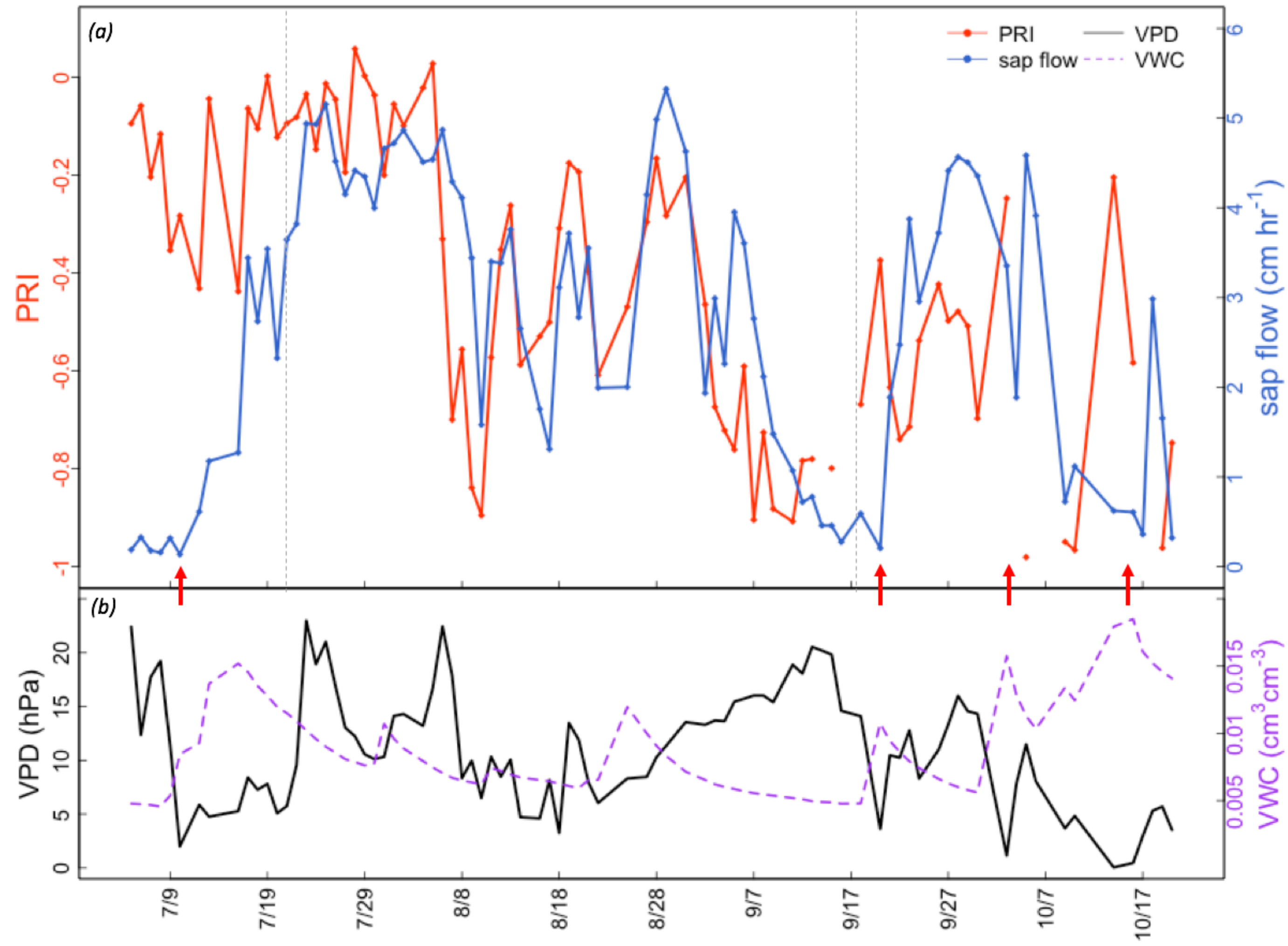
| ***Model*** | ***PRI*** | ***GPP*** |
|---|---|---|
| VWC | .17*** | 0 |
| $T_{air}$ | .10** | .08* |
| VPD | 0 | .13** |
| PPFD | 0 | 0.02 |
| VWC + $T_{air}$ | **0.4*** ** | .12** |
| VWC + VPD | .18*** | **.18*** ** |
| VWC + PPFD | .17*** | 0.03 |
| VWC + $T_{air}$ + PPFD | .4*** | .12** |
| VWC + VPD+ PPFD | .18*** | .18*** |

*Table 1: Hierarchical regression analysis for predictors of PRI and GPP. Values presented are correlation of determination ($R^2$). *$p < 0.05$ ** $p<0.01$ ***$p<0.001$.*

### *3.3 Seasonal PRI & Sap flow*

Our assertion that PRI tracks seasonal water dynamics is further supported by sap flow analysis. Over the monsoon season, PRI and sap flow varied in synchrony (*see Fig 4a*). This was especially true from late July through mid-September, when PRI and sap flow were positively correlated with $R^2$=0.55 (*see Fig 4c*). During rain events with extremely low VPD (*see Fig 4b*), sap flow response exhibited a ~2 day lagged response behind PRI (*see red arrows in Fig 4*).

GPP association with seasonal sap flow was dramatically weaker (*see Fig 5a*). Sap flow and GPP were not significantly related throughout the season ($p>0.05$). In July and August when PRI vs GPP had a negative relationship (*Fig 2b,c*), GPP and sap flow had no relationship ($p>0.05$; *see Fig 5b*); while in September when PRI vs GPP were positively correlated (*Fig 2b,d*), GPP and sap flow were also positively correlated ($p<0.05$, $R^2$=.63; *see Fig 5c*).



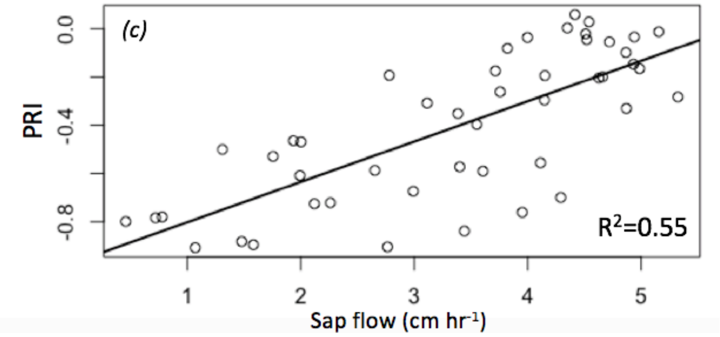


*Fig 4: a) Seasonal course of PRI compared with sap flow (cm hr$^{-1}$) from July-October compared with b) changing VPD (hPa) and VWC (cm$^3$cm$^{-3}$) during that time. Red arrows indicate a time lag of sap flow following PRI response. c) regression analysis for data between dotted lines in Fig 4a–which excludes times that exhibit a temporal lag—shows PRI and sap flow are positively correlated ($R^2$=.55, $p<0.05$).*

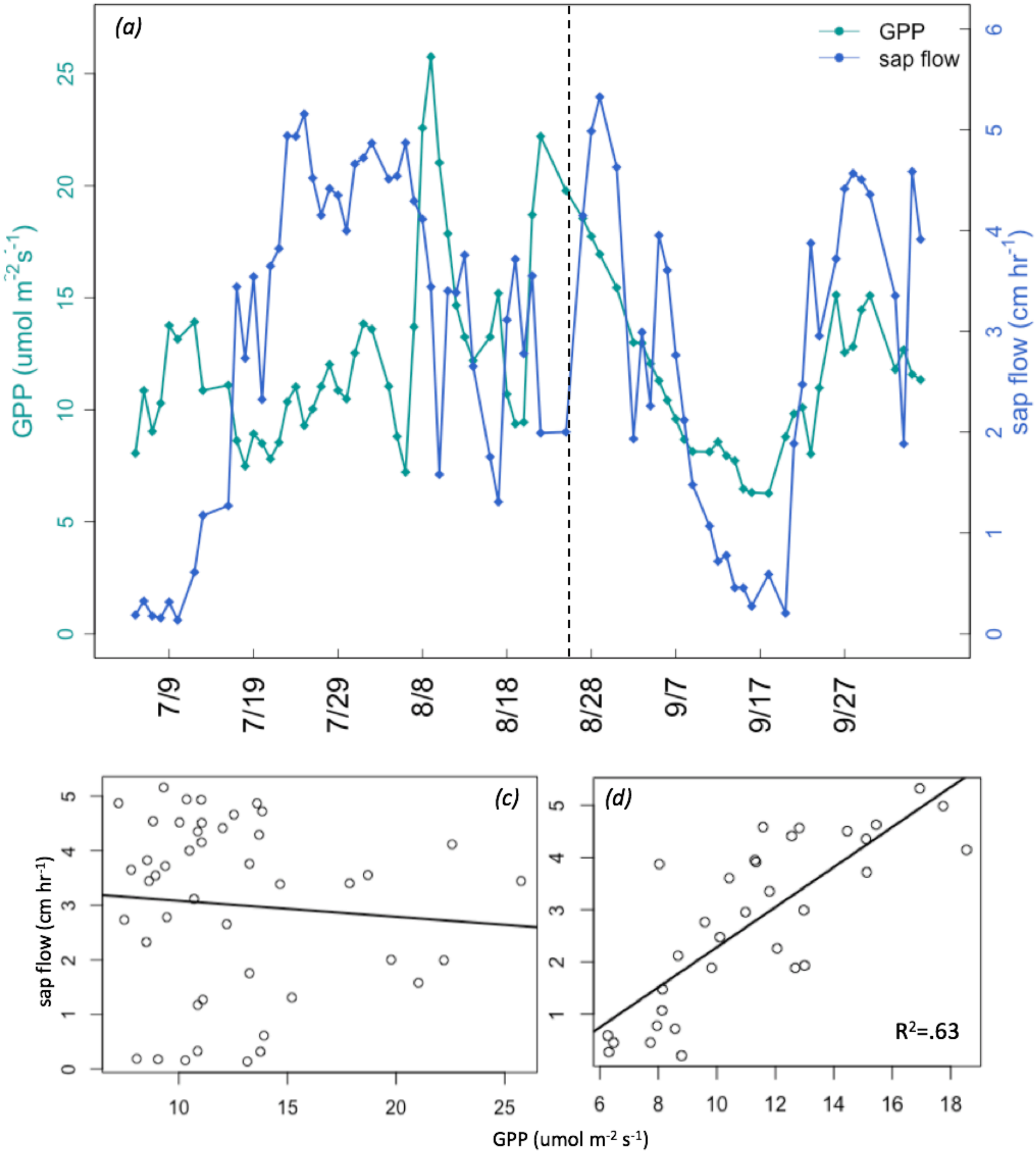


*Fig 5: a) Seasonal course of GPP ($\mu mol\ m^{-2}s^{-1}$) relative to sap flow ($cm\ hr^{-1}$) had an overall insignificant relationship ($p>0.05$, $R^2=.05$). When the season was divided at the same point as in Fig 2b, b) July and August showed a non-significant relationship, c) while in September sap flow and GPP were positively correlated ($p>.05$, $R^2=.63$).*

### *3.4 Diurnal Canopy Scale PRI*

For diurnal analysis, data from mid-season, July 23-Sept 16, were used to calculate 30min averages. All data was used where PPFD > 500 µmol $m^2$ $s^{-1}$, from 9:00am – 1:30pm when sun-sensor angle was <40°. Constancy of diurnal dynamics was tested by plotting each variable against SZA (*see Table 2*). Canopy scale diurnal data showed no significant diurnal signal in PRI, LUE, or GPP ($p>0.05$; *see Fig 6*). PRI was not significantly related to GPP ($p>.05$) or PPFD ($p=.08$, $R^2=.34$), and PRI was significantly negatively related to LUE ($p<0.05$, $R^2=.48$, *Table 1*), contrary to expectations. PPFD values show that the system exists in a state of extremely high irradiance and appears to be light saturated throughout much of the day, with daily average PPDF >1200 µmol $m^{-2}s^{-1}$ from 8:30am – 3:00pm (*see Fig 6*).

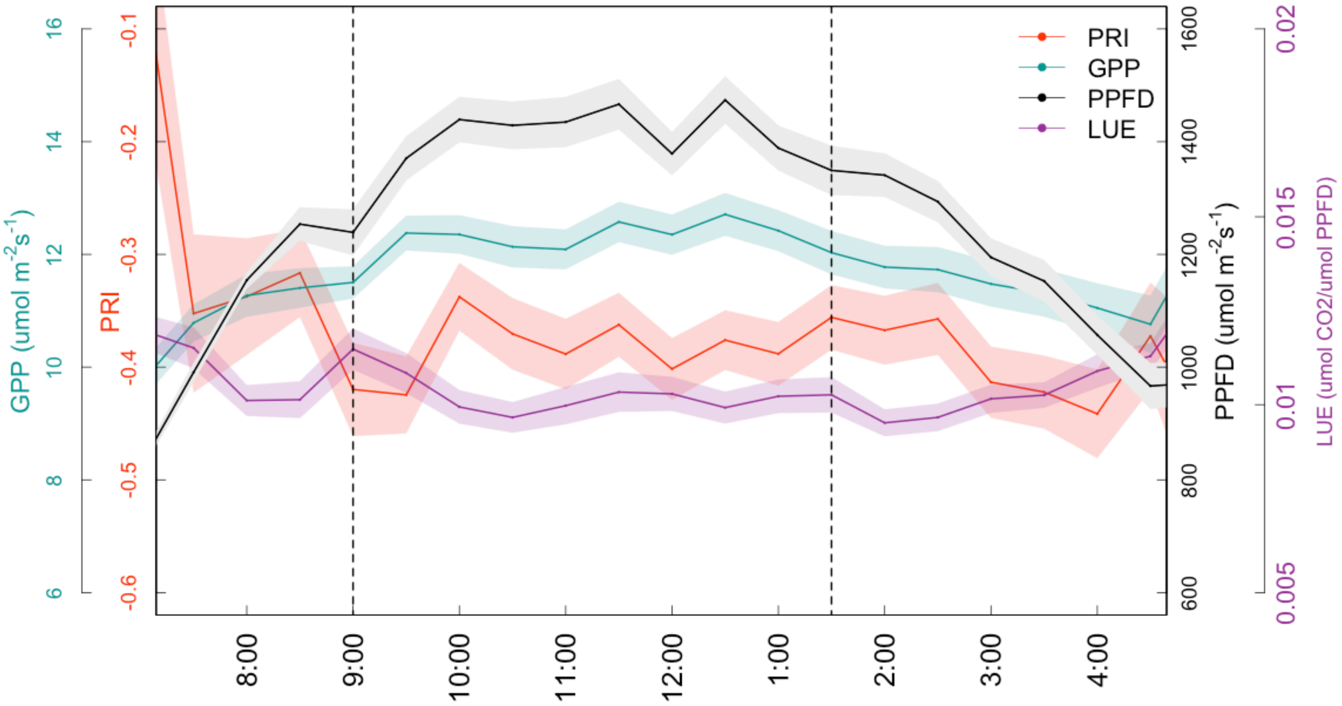


*Fig 6: Half-hourly diurnal PRI, GPP (µmol $m^{-2}s^{-1}$), LUE (µmol $CO_2$/µmol PPFD), and PPFD (µmol $m^{-2}s^{-1}$) averaged from day of year 203-260 (July 23- Sept 16). All data are included where PPFD>500 µmol $m^{-2}s^{-1}$. Dotted lines at 9:00am and 1:30pm indicates when sun-sensor angle <40° for eastern facing needles. Error represents ±1SE from the mean.*

| | **PRI** | **$T_{air}$** | **PPFD** | **LUE** | **GPP** |
|---|---|---|---|---|---|
| **PRI** | | | | | |
| **$T_{air}$** | *0.28* | | | | |
| **PPFD** | *0.34* | ***0.44**** | | | |
| **LUE** | ***-0.48**** | ***-0.52**** | ***-0.69***** | | |
| **GPP** | *0.11* | ***0.41**** | ***0.69***** | *-0.31* | |
| **SZA** | *-0.15* | ***-0.94****** | *-0.27* | *0.35* | *-0.35* |

*Table 2: Correlation matrix for diurnal data for sun-sensor angle <40° and PPFD> 500 μmol m$^2$ s$^{-1}$. Values presented are correlation of determination ($R^2$).* $^*p < 0.05$ $^{**}p<0.01$ $^{***}p<0.001$.

*3.5 Leaf Level Diurnal PRI*

We chose to conduct leaf level analyses in top-of-canopy sunlit leaves with the hypothesis that upper canopy layers would demonstrate large gradients in PRI due to strong photoprotective needs (Lichtenthaler et al. 2007). Branch data were aggregated to give hourly data for each species, therefore each data point represents an average of 1-4 measurements. Gsw and $A_{net}$ both responded to diurnal changes in VPD and $T_{air}$ (*see Fig 7a,b*), and we expected that the xanthophyll pool, which regulates the amount of energy being used for electron transport, would respond in concert. However, in agreement with canopy data (*Fig 6*), leaf PRI did not express a diurnal signal for either *P. ponderosa* or *P. strobiformis* (p>0.05; *see Fig 7g*). Constancy of diurnal dynamics was tested by plotting each species against PAR. Significant noise in diurnal leaf level PRI is not an uncommon issue (Dobrowski et al. 2005).

In addition, NPQ was remarkably high by early morning, with values >3 by 9:00am, and remained high throughout the day (*see Fig 7c*). High NPQ values were supported by correspondingly low ΦPSII values. That *P. strobiformis* appeared to have higher NPQ and lower ΦPSII resulting in lower LUE and $A_{net}$, indicates that this species was experiencing a higher degree of stress induced reductions in photosynthetic function compared to *P. ponderosa.* Though diurnally constant for both species, PRI appeared to be, for the most part, lower in *P. strobiformis* than in *P. ponderosa,* indicating that PRI was able to differentiate between species.

However, we cannot not conclude statistically that PRI differed significantly between the two species (two-sample T-test, p=.08), likely due to a limited sample size.

Tower and leaf level data showed that these needles exist in a remarkably high light environment (*Fig 6, 7f*)—higher than reported in most other studies. Yet, natural vegetation is remarkable at adapting to its natural light environment (Walters 2005). The Fv/Fm parameter should be 0.83-0.84 in most species (Bjorkman and Demmig 1987), while reductions in Fv/Fm indicate photoinhibition has occurred in response to prolonged stress (Maxwell and Johnson 2000). Average Fv/Fm for *P. ponderosa* was 0.845±0.004 and for *P. strobiformis* was 0.837±0.002. These needles were not experiencing any sustained photoinhibition and the plants' ability to dissipate excess light energy was within the capacity of reversible photoprotective pathways.

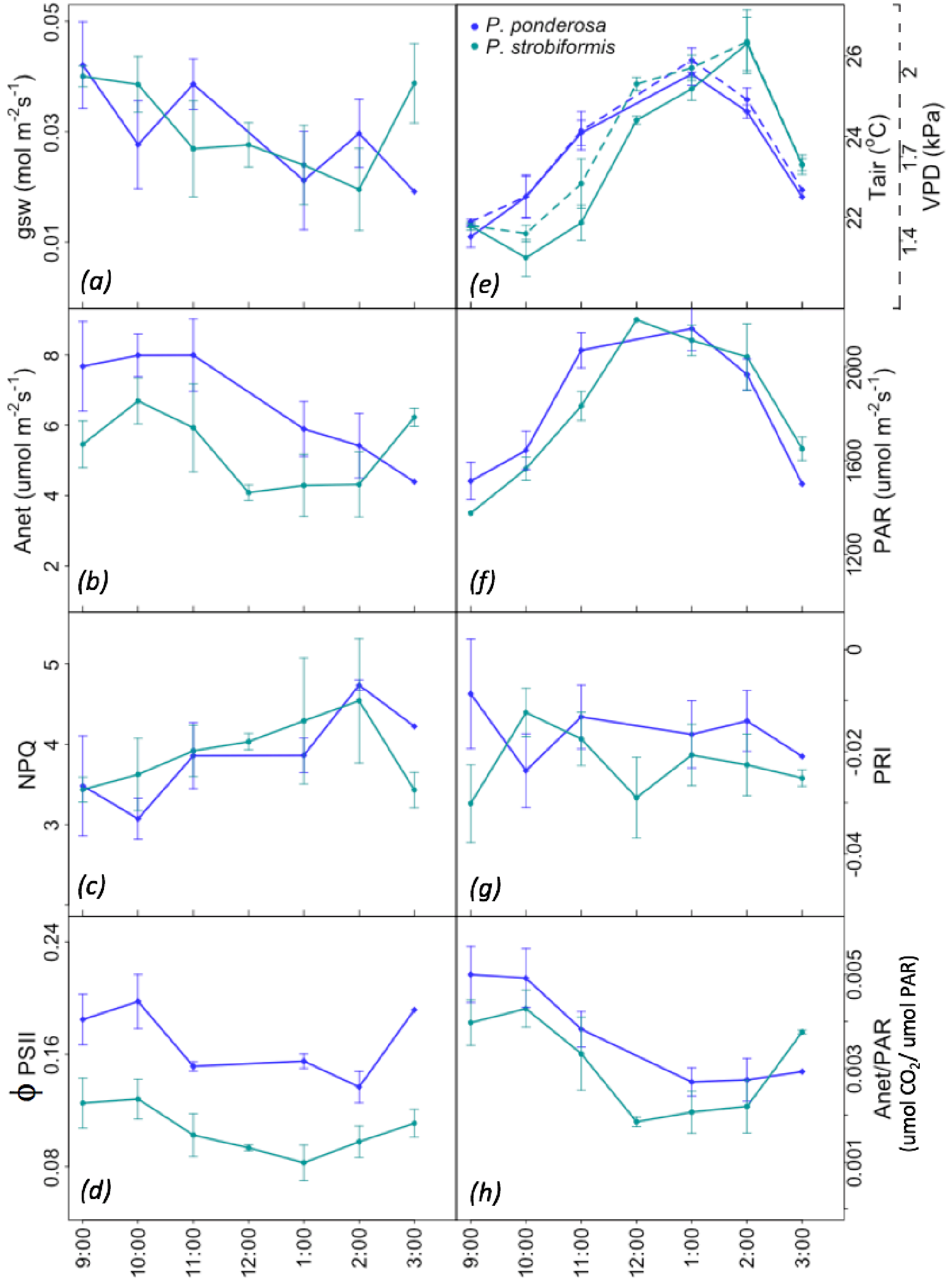


*Figure 7: Leaf level hourly diurnal data for a) gsw (mol $m^{-2}s^{-1}$) b) $A_{net}$ (μmol $m^{-2}s^{-1}$) c) NPQ (unitless), d) ϕPSII (unitless), e) $T_{air}$ (°C, solid lines) and VPD (kPA, dotted lines), f) PAR (μmol*

*m*$^{-2}$*s*$^{-1}$*), f) PRI, and h) LUE calculated as* $A_{net}$*/PAR (μmol* $CO_2$ */μmol PPFD). Each point is an average of 1-4 branches, (some missing data due to cloudiness), and was a measurement of 20 needles for P. strobiformis (green) and 12 needles for P. ponderosa (blue). Error bars represent ±1SE from the mean.*

# 4. DISCUSSION

Remotely sensed PRI holds potential to fill a major gap in our ability to distinguish how water availability influences C dynamics, particularly in evergreen conifer forests, but has largely been under-studied in natural wildlands. In this study, we assessed spectral measurements in conjunction with biophysical and functional parameters for a deeper examination of PRI as a proxy for dynamic photoprotection.

## *4.1 Inconsistent PRI-GPP seasonal relationships*

While a number of studies have attempted to relate PRI to canopy level productivity using flux data, we still lack a mechanistic understanding of the drivers involved and how these relationships vary between ecosystems. Results from the literature on the seasonal dynamics of PRI are inconclusive and a strong relationship between PRI and LUE may (Cheng et al. 2013; Louis et al. 2005; Nichol et al. 2002; Serrano and Penuelas 2005) or may not be observed (Filella et al. 2004; Gamon et al. 2001; Nakaji et al. 2006; Rahimzadeh-Bajgiran et al. 2012; Soudani et al. 2014). Median $R^2$ for 15 seasonal relationships between LUE and PRI for conifer individuals or stands reported in the literature was $R^2$=0.65 (Zhang et al. 2016), however most of these studies were in boreal climates or potted plants. He et al. (2016) showed that GPP modeled from MODIS-based PRI was able to predict measured GPP at flux tower sites across the continental U.S. (.46> $R^2$>.82), but model performance in arid or semi-arid evergreen needleleaf forests was much lower ($R^2$=.30).

Only a few studies of seasonal PRI have been conducted in forests that experience a monsoon climate, and those have reported inconsistent and weaker relationships with estimates of productivity (Nakaji et al. 2014; Nakaji et al. 2006; Zhang et al. 2015). In agreement, our results show that the relationship between PRI and GPP varies dramatically throughout the monsoon growing season. However, while Nakaji et al. (2006) attributed a negative PRI-LUE relationship to yellowing deciduous needles, the inverse PRI-LUE relationship in our system occurs during the period leading up to peak productivity, and therefore cannot be explained by any obvious state change such as senescence. Changing hydrologic variability is one explanation. July and August, which mark the beginning and peak of the monsoon, experience an overall wetter environment with frequent rain events creating more variable hydrologic dynamics. In contrast September is relatively drier, moving towards the end of the monsoon season (*Fig 2a*). In agreement with this explanation, time periods with high frequency rain events and frequent alternations between sunny and cloudy conditions have been linked to scattered relationships between PRI and LUE (Soudani et al. 2014; Zhang et al. 2015). Indeed, Zhang et al. (2015) found significant negative PRI-LUE relationships around days with heavy precipitation events in a sub-tropical conifer forest, with PRI and LUE being correlated on 40% of dry season days but only 22% of rainy season days.

On the other hand, the seasonal break down in the PRI-GPP relationship may be driven by physiological mechanisms. There is substantial evidence that changing carotenoid to chlorophyll (Car/Chl) ratios can dominate the seasonal PRI signal (Filella et al. 2009; Frechette et al. 2016; Gitelson et al. 2017; Hmimina et al. 2015; Porcar-Castell et al. 2012; Sims and Gamon 2002; Stylinski et al. 2002; Wong and Gamon 2015b) masking its relationship to changing deepoxidation state (DEPS). The PRI relationship with short-term, reversible changes in DEPS has been termed the “facultative” component, while its confounding relationship with long term changes in Car/Chl has been termed the “constitutive” component (Gamon and Berry 2012). This pattern is due to the fact that both carotenoids and chlorophylls absorb at 531nm, while chlorophylls but not carotenoids absorb at 570nm. When seasonal photosynthetic activity is regulated by changing Car/Chl ratios in response to changing environmental stress, this confounding effect may actually magnify the seasonal relationship between PRI and LUE (Gamon and Berry 2012; Wong and Gamon 2015a). On the other hand, when photosynthesis is decoupled from the timing of these pigment pool changes, there can be a concurrent decoupling in the seasonal PRI-LUE relationship (Frechette et al. 2015; Porcar-Castell et al. 2012). It is possible that the observed decoupling between PRI and GPP represents a shift in pigment pool composition. During the prolonged pre-monsoon drought, we might expect sustained forms of NPQ to dominate, therefore pigment pool adjustments following the start of the monsoon rewetting in early July may be decoupled from photosynthetic recovery. To test this hypothesis, PRI data that extend into the pre-monsoon season should be analyzed in conjunction with a seasonal pigment composition analysis.

### *4.2 Seasonal PRI responds to ecohydrological dynamics*

Analysis of long-term EC records at our site indicates that this forest, subject to a high degree of interannual climatic variability, can be both water and/or energy limited (unpublished data, J. Knowles) depending on prevailing conditions. Our result that PRI was driven by a combination of VWC and $T_{air}$ provides further evidence of this, and indicates that PRI is able to integrate across ecosystem response to multiple environmental drivers. In addition, PPFD did not appear to be as important in determining either PRI or gross $CO_2$ flux as expected, likely due to light saturation and in agreement with Sims et al. (2005). Our results are supported by previous studies which found PRI varied seasonally in response to $T_{air}$ in conifers (Nakaji et al. 2006; Wong and Gamon 2015a). However, in contrast, PRI has been shown to be uncorrelated with $T_{air}$ for evergreen needleleaf sites across the continental U.S. (He et al. 2016), and weakly correlated with $T_{air}$ in a subtropical conifer forest (Zhang et al. 2015). These inconsistencies are unsurprising and reflect varying degrees of temperature limitation across diverse ecosystems.

In combination with energy constraints, we showed that PRI responded to dynamic water availability. Studies in crop systems have shown that soil moisture can affect the PRI relationship with LUE (Inoue and Penuelas 2006) or irradiation (Magney et al. 2016), and these effects become stronger as soil moisture becomes increasingly limited. It is logical that unnatural crop systems would be highly responsive to water availability– however expected PRI response to water availability in natural forests is more complex. PRI was found to be driven by stress response to reduced soil moisture in a beech forest (Nestola et al. 2018), while in contrast, using MODIS sPRI13 as a proxy for water supply to improve modeled estimates of GPP was less effective in forested systems due to the complex ecohydrology of large trees (He et al. 2016). We found that during the time period with lowest VWC in our study (mid-September), PRI appeared more strongly driven by water availability than by $T_{air}$ (*Fig 3a*). The overall moderately low performance of the MLR ($R^2 = .41$), indicates that the relative strengths of $T_{air}$ and VWC as drivers are dynamic through time and complicated by threshold-type responses. PRI response to environmental drivers appears to be highly site specific due to contrasting evolutionary adaptation to constraints on C assimilation (Garbulsky et al. 2011). That being said, our result that PRI can be predicted using an MLR with VWC and $T_{air}$ as predictors agrees with what we believe to be limiting constraints in our study system.

The results of the MLR analysis are strengthened by sap flow data which show that PRI was significantly related to transpiration across the season. Because gsw simultaneously regulates water loss and $CO_2$ uptake (Collatz et al. 1991; Meinzer 2002), transpiration rates should be related to photosynthetic inhibition as measured by PRI. While a few studies in crop systems have attempted to link seasonal PRI to measures or proxies of plant hydraulics (Magney et al. 2016; Rossini et al. 2013; Suarez et al. 2008; Sun et al. 2014; Zarco-Tejada et al. 2012), even fewer have attempted to relate PRI to sap flow rates (Manzanera et al. 2017; Marino et al. 2014). PRI has been shown to vary with $T_{air}$-$T_{leaf}$—a proxy for transpiration—in crop systems (Rossini et al. 2013; Suarez et al. 2008), and has been used as a remotely sensed proxy of gsw to successfully model transpiration (Hilker et al. 2013). Our results agree with Marino et al. (2014) who showed a linear relationship between sap flux density and leaf-level PRI in olive trees ($R^2$=.42), and Manzanera et al. (2017) who showed that single-tree scale PRI was significantly correlated with sap flow rate ($R^2$=.62) in juvenile potted pines. However, this is the first study to our knowledge to report a relationship between PRI and sap flow in a natural mature forest, the first to do so using canopy PRI, and the first to show this relationship on a seasonal time scale with continuous, daily resolution. As Magney et al. (2016) reported on a diurnal scale, we report on a seasonal scale and in a natural system that stomatal opening is regulated similarly as PRI. These sap flow results suggest that on a seasonal scale PRI is an effective indicator of stomatal response to ecohydrological dynamics.

The influence of precipitation pulses in semi-arid ecosystems causes functional parameters to decouple over relatively short time scales (Huxman et al. 2004). While we found that PRI sometimes responded prior to transpiration, Zarco-Tejada et al. (2012) reported the opposite time delay, with PRI responding slightly behind $T_{canopy}$-$T_{air}$ during drought recovery after re-watering. The important difference is that our study system experienced re-watering due to rain events, which simultaneously affected the VPD and radiation intensity of the system, whereas their system experienced re-wetting from irrigation independent of atmospheric conditions. We attribute the exhibited temporal lag in our study to time periods with extremely low VPD corresponding to rain events (*see Fig 4b*). During these times, transpiration slows to a minimum because evaporative demand is too low to drive the physical pull of water. Therefore, these instances of low VPD represent times when transpiration is low yet leaves are relieved of stress, resulting in a PRI response to unstressed conditions and sap flow following only after the water potential gradient is reestablished.

We highlight that both our study and Manzanera et al. (2017) observed a relationship between PRI and transpiration in pine species when a significant relationship between PRI and $CO_2$ assimilation was absent. We would expect that PRI is related to gsw only when diffusional limitations cause photosynthetic inhibition—meaning PRI should be related to $CO_2$ assimilation if it is also related to transpiration, contrary to our results. Remote sensing of transpiration remains a nascent field (Damm et al. 2018; Marshall et al. 2016), and the way in which the PRI signal interacts with water use efficiency dynamics is entirely unclear and warrants further study. Lacking a physiological explanation, we assess methodological inconsistencies. Another surprising result was that PRI performed much better than GPP at tracking the three-month time course of sap flow, and when GPP did track sap flow in September (*Fig 5*), was the same time period GPP and PRI were positively correlated (*Fig 2*). These results lead to the speculation that a footprint mismatch is at play. The size of any flux tower footprint varies with atmospheric stability and can change monthly (Chen et al. 2009), and spatiotemporal mismatches are a recognized issue when attempting to pair optical and flux methods (Chen et al. 2009; Gamon et al. 2010; Gamon et al. 2006; Pacheco-Labrador et al. 2017). While the FOV of the SRS sensor is ~50m$^2$, EC measurements at this site come from within ~750m. Spatial variability of PRI has been shown to be affected by species (Atherton et al. 2017; Guo and Trotter 2004), and the species within the SRS sensor FOV are not fully representative of the demography within the entire flux tower footprint, as it excludes *P. menziesii*. On the other hand, the SRS sensor measured the full or partial canopy of five trees, four of which were used to measure sap flow. Therefore, the spatial scales of PRI and sap flow measurements were nearly identical, which we believe contributes to their close correlation even when PRI was not closely correlated to $CO_2$ assimilation.

Our results in conjunction with previous studies demonstrate that PRI holds remarkable potential as a unique remotely sensed indicator of ecohydrological constraints. Remote sensing has proven to be a powerful tool for monitoring past and ongoing ecosystem disturbances such as drought induced forest mortality, however to harness the full potential of these technologies, progress should be made in our ability to predict when ecosystems will be vulnerable to future degradation prior to visible manifestations (Smith et al. 2014). PRI has potential as an a priori approach for characterizing plant response to future changes in hydroclimate.

### *4.3 Suppressed Diurnal PRI response*

Photochemical efficiency should parallel irradiance conditions throughout a diurnal cycle (Demmig-Adams et al. 2012). Characterization of diurnal PRI is needed if snapshot satellite data can ever serve as a robust representation of photosynthetic processes (Sims et al. 2005), yet at present, information of diurnal PRI is limited in natural systems, particularly in mature conifer forests (Gamon and Bond 2013; Mottus et al. 2018).

Very few studies have used canopy PRI to track diurnal changes in conifer forests (Zhang et al. 2016). Other studies, in agreement with our results, have found that diurnal dynamics were suppressed in summertime (Cheng et al. 2009; Middleton et al. 2009), indicating that canopy PRI may fail to exhibit diurnal variation when multiple environmental stressors occur in concert with high light intensities, or anytime diurnal LUE variability is low. To probe more deeply into the physiological meaning behind a constant PRI, we turn to the leaf level analysis. This is the first study to our knowledge to analyze diurnal needle PRI and its relationship with both gas exchange and fluorescence parameters in top of canopy needles of a montane conifer forest.

Across many species and plant functional types, there is conclusive evidence of a strong correlation between leaf PRI and ΦPSII as well as LUE (for reviews see Garbulsky et al. 2011; Zhang et al. 2016). However, most diurnal leaf level studies have been biased towards broadleaved and herbaceous plants. Of the 57 PRI-ΦPSII relationships analyzed in Zhang et al. (2016) metanalysis, only four were for conifers from a single study of *Pinus taiwanensis* (Weng et al. 2012). In addition, leaf PRI should track the PAM fluorometry parameter NPQ on diurnal time scales (Alonso et al. 2017; Atherton et al. 2016; Evain et al. 2004; Gamon et al. 1992; Rahimzadeh-Bajgiran et al. 2012), however this relationship has proven to be complex and is often non-significant (Garbulsky et al. 2011). No other studies to date have analyzed the diurnal relationship between PRI and NPQ in conifer needles.

We found that PRI did not predict diurnal LUE for either species. PRI should be a proxy of LUE when ΦPSII determines the rate of C assimilation (Guo and Trotter 2004). We might expect ΦPSII to be uncoupled from C assimilation under conditions of severe stress. Stress conditions can decouple electron transport in the light reactions from carboxylation in the dark reactions via alternative electron sinks (Porcar-Castell et al. 2014). This would by extension manifest as an uncoupling between PRI and $CO_2$ assimilation (Kovac et al. 2018). In our study, ΦPSII and $A_{net}$ were significantly correlated in *P. strobiformis* ($p<0.05$, $R^2=.62$), but not in *P. ponderosa.* This suggests that *P. ponderosa* is utilizing alternative processes that reduce energy for use in photosynthesis as a form of stress relief, which impedes the ability of PRI to predict LUE. While neither species expressed a statistically significant diurnal PRI signal, it appears that *P. strobiformis* may have been more diurnally variable than *P. ponderosa* (*Fig 7g*), in agreement with these theories. Larger sample size would be needed to investigate these relationships more conclusively.

Typically, conifer species adapted to persist through repeated unfavorable seasons experience reduced Fv/Fm during winter downregulation when sustained levels of Z+A remain engaged for energy dissipation (Demmig-Adams and Adams 2006; Demmig-Adams et al. 2012; Porcar-Castell 2011). The lack of diurnal PRI signal combined with the fact that PAR and NPQ are very high by early morning while ΦPSII is quite low (*Fig 7*), indicates that these top-of-canopy needles exist in a state of maximum photo stress throughout the entire day. This suggests that Z+A is retained overnight similar to overwintering pines, but importantly, without the concurrent reduction in Fv/Fm. Retention of Z+A without a reduction in Fv/Fm was first reported by Barker et al. (2002) for Yucca species withstanding extreme summers in the Mojave Desert, leading to the discovery that Z + A retention and Z + A engagement are separate processes. Because irradiance remains saturated all day, these needles may have adapted to forgo unnecessary epoxidation of Z + A in the morning and afternoon so that zeaxanthin can be more rapidly engaged upon early morning exposure to high light than if violaxanthin had to first be de-epoxidized. Because PRI detects conversion to V to Z+A, but not engagement of already present Z+A, retention of Z+A will decouple PRI from diurnal photoprotection. Contrary to

Mottus et al. (2018) who attributed constant PRI to a lack of photosynthetic downregulation in a boreal forest, we hypothesize that constant PRI decoupled from diurnally changing $A_{net}$ indicates xanthophyll cycle pigments are retained in Z+A form, but maintain flexibility in terms of engagement and disengagement. Ongoing xanthophyll pigment biochemical analysis will be processed to test this hypothesis. Overall, we find an instantaneous measurement of canopy PRI would not be representative of instantaneous photosynthesis in this system.

Leaf and canopy scale diurnal analysis each have their own limitations, therefore complimenting one with the other can strengthen conclusions. A major limitation of any leaf level analysis is the pooling of data from measurements across multiple leaves and branches on different days. Leaf-leaf heterogeneity in orientation (Mottus et al. 2018), Car/Chl ratios, or physical structure (Marin et al. 2016) could obscure the diurnal PRI signal (Ac et al. 2009). However, canopy scale PRI integrates over this inter-leaf heterogeneity. On the other hand, physical factors complicate the acquisition of canopy scale diurnal PRI, including sun sensor geometry effects on illumination (Barton and North 2001; Grace et al. 2007; Hall et al. 2008; Hilker et al. 2008a), mixed-pixel background effects, as well as canopy structural effects (Hernandez-Clemente et al. 2016; Hernandez-Clemente et al. 2011; Jia et al. 2018). Barton and North (2001) showed that PRI exhibits greater variation of view angle than most other vegetation indices, and this has been one of the more significant barriers to moving PRI out of the proof-of-concept stage. These complicating effects can uncouple canopy PRI from leaf physiology. Therefore, agreement between leaf-level measurements that are not subject to structural and geometrical effects and canopy-level measurements that integrate over leaf heterogeneity, strengthen our confidence that the demonstrated lack of PRI diurnal response is in fact rooted in physiology.

# 5. CONCLUSIONS

We found that the ability of PRI to serve as a proxy for seasonal and diurnal environmental photoprotection in a semi-arid conifer forest was highly dependent on temporal scale. At the canopy scale we found that the relationship between PRI and GPP changed over the course of the monsoon season. This could be due to a) high frequency rain events b) changing pigment pools following the transition out of pre-monsoon sustained suppression, or c) a footprint mismatch between EC flux and optical data. In addition, we found that seasonal PRI responded to ecohydrological dynamics as expected in a system that is both water and energy limited, and reported for the first time a relationship between seasonal PRI and sap flow in a natural, mature forest. On a diurnal time scale we conclude that PRI remained constant throughout the day, and hypothesize that in this high light, high temperature environment, retention of zeaxanthin through day and night keep top of canopy needles poised for flexible engagement.

Few studies have been done in systems that exhibit a bimodal pattern of production, or in conifer forests that retain winter photosynthetic capacity. We suggest that to investigate further, this analysis should be repeated multiple times throughout the season, paying particular attention to the transition between pre-monsoon drought and monsoon re-wetting. Seasonally iterated diurnal analysis should be paired with biochemical characterization of the DEPS of the xanthophyll cycle and total Car/Chl pools to help discern if PRI is representing xanthophyll cycle activity versus larger pigment pool changes. We hypothesize that complex temporal phase decoupling may be present between PRI, transpiration, GPP, and pigment composition during the atypical seasonal transitions of this semi-arid forest (Ruehr et al. 2012). Ultimately this investigation will help elucidate how the presence of water stress complicates seasonal PRI-LUE relationships, and may serve as a window into the future for forests across the western U.S. expected to undergo significant hydroclimatic changes.

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# APPENDIX B

## ADDITIONAL FIGURES

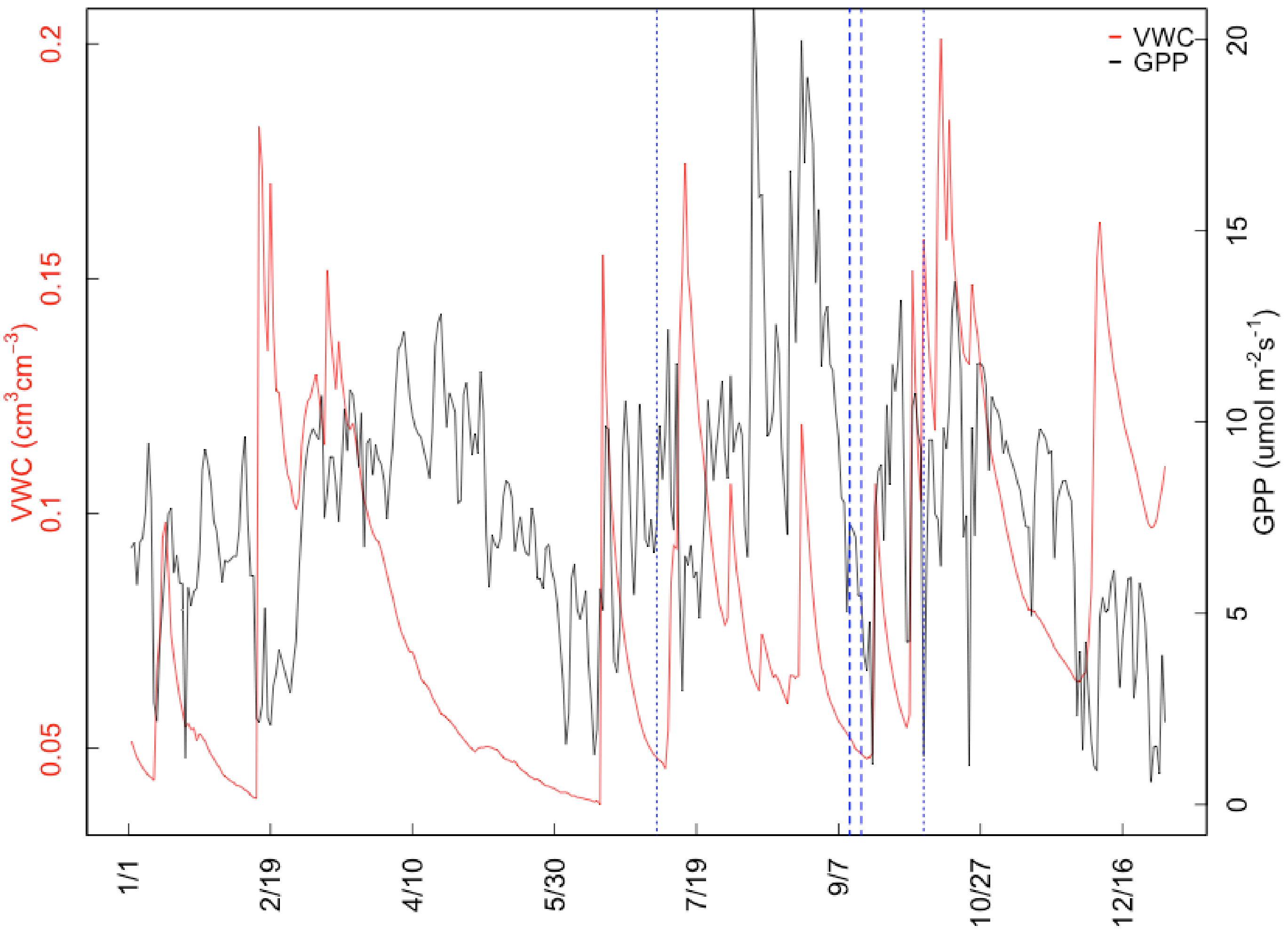

*Fig 8: 2018 annual course of GPP and VWC for context. Dotted blue lines indicates time frame of canopy-scale analysis from DOY 186-279. Dashed blue line pair indicates time frame of leaf level analysis on Sept 13-14.*

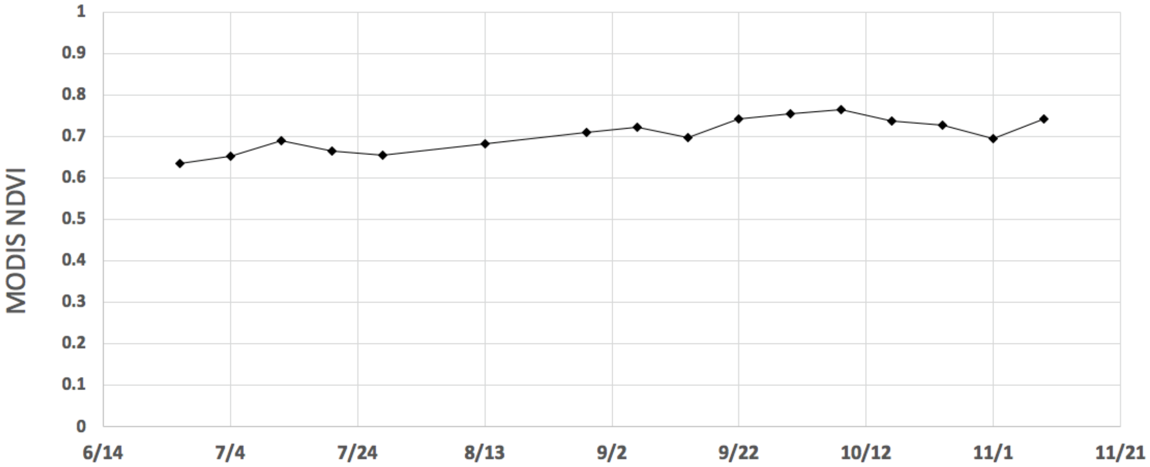

*Figure 9: MODIS NDVI time series data during the study period, 2018. Data was acquired from Terra MOD13Q1(Didan 2015a) and Aqua MYD13Q1(Didan 2015b) surface reflectance products. The spatial resolution is 250m. Data downloaded from MODIS and VIIRS Land Products Global Subsetting and Visualization Tool. ORNL DAAC, Oak Ridge, Tennessee, USA.*

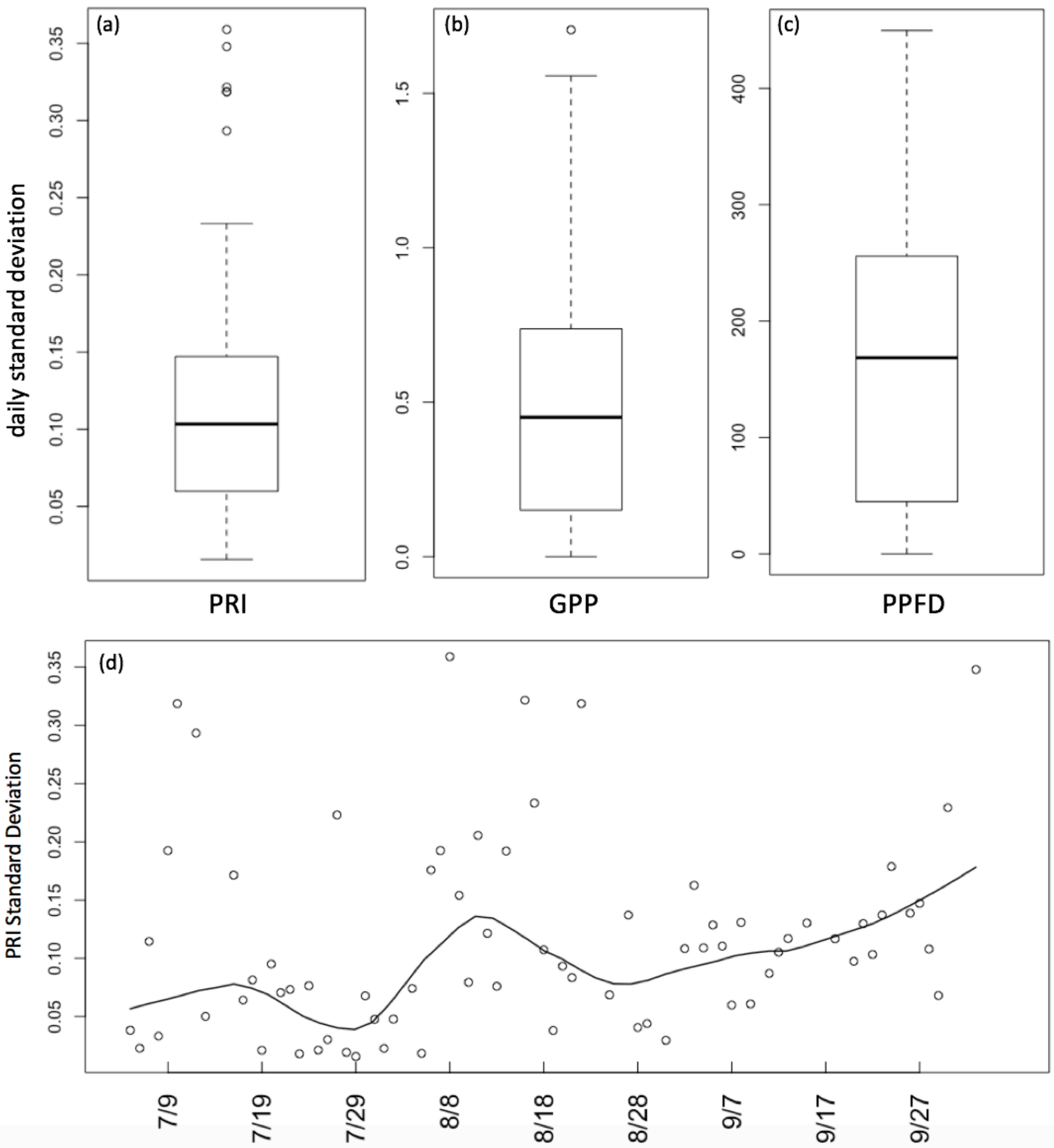

*Figure 10: The spread of standard deviations for each daily mean from 10:00 – 12:00 for PPFD >1000 μmol* $m^2s^{-1}$ *is shown for seasonal a) PRI, b) GPP, and c) PPFD; and d) seasonal changes in the standard deviation of PRI daily means.*

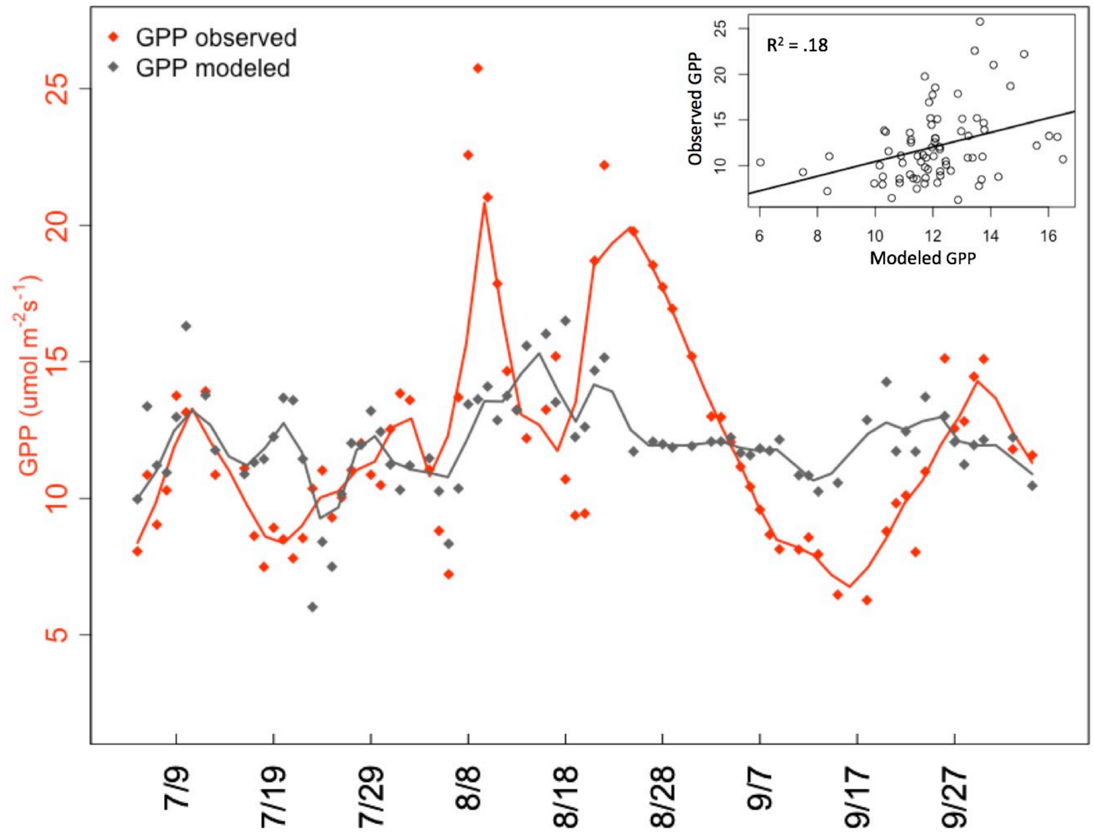

*Figure 11: Observed GPP plotted with GPP modeled from the cross-validated MLR model using VWC and* VPD *as predictors. Inlay shows regression between observed values and PRI modeled from a 5-fold cross validation ($R^2$ = .18, $p<0.05$).*