

PATTERNS OF PRIMARY PRODUCTIVITY IN A SEMIARID MONTANE FOREST

By

Patrick Murphy

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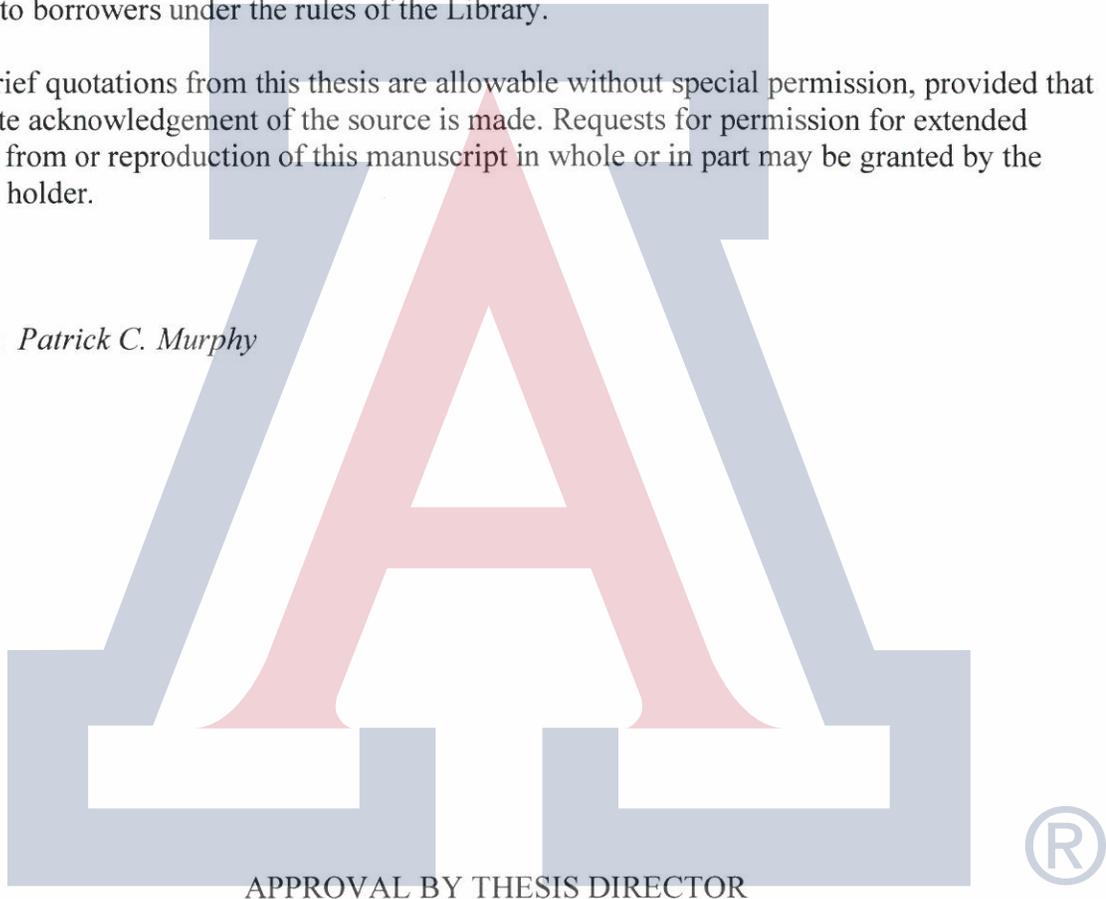
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This thesis has been approved on the date shown below:

Greg Barron-Gafford *5/2/18*
 Greg Barron-Gafford Date
 Associate Professor in the School of Geography and Development

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ABSTRACT

Global forests are projected to be impacted by changing climate, but the scientific community is working to constrain considerable uncertainty in the extent of these impacts. In the southwestern United States, semiarid forests are important natural and social resources, but they face a decline in productivity. One challenge associated with modeling and projecting changes to forest function into the future is understanding controls on current processes at the sub-landscape scale. Because many of these southwestern forests are found in mountainous regions, complex terrain adds to the challenge of characterizing this productivity beyond individual trees. In this study, we attempt to quantify the effect imposed by topographic aspect on primary productivity by observing three co-dominant native species. Repeated measurements of net carbon assimilation demonstrate that *P. ponderosa* and *P. strobiformis* respond to natural differences in volumetric water content across opposing north and south aspects, while *P. menziesii* does not behave this way. The implications of these results are important to modeling potential carbon uptake and transpirative water demand in regions where these species dominate.

INTRODUCTION

Background

The changing climate associated with increases in anthropogenic carbon dioxide has drawn greater attention to the Earth's carbon cycle and the role of vegetation in removing and storing carbon. Understanding the role of the terrestrial biosphere in carbon cycling is important to reducing uncertainty in projections of the impacts of climate change, and to managing carbon through land use. Further research into ecosystem function and resilience will better prepare modelers to address these uncertainties, and we need more details and data on ecosystem function to address the paucity of inputs into Earth system models. There are multiple large-scale uncertainties in constraining the global carbon budget, including the magnitude of the carbon sink potential of North American Forests (Myneni et al. 2001) under current and projected climatic changes. Maintaining and increasing carbon uptake by forests and other land uses is an important component of the United States' commitment to reducing greenhouse gas emissions.

At local levels, the controls on vegetation carbon uptake in different ecosystems are only partly understood, especially as climate change itself alters ecosystems, and this aggregates to uncertainties in the role of terrestrial ecosystems in the global carbon cycle. Among the variables that influence carbon uptake locally are soil, species mix, moisture, temperature and energy inputs. Several of these vary by aspect and season – influences that are poorly understood in terms of carbon exchange.

Much of the anthropogenic influence on the function of our biosphere arises from the increase in concentration of carbon dioxide (CO₂) in the atmosphere associated with the burning of fossil fuels and the loss of forests. This rise is a major contributor to the net increase in global surface temperatures, yet debate about how extensively this increase will affect the future climate

remains an active part of scientific discourse. The scientific community has established that, currently, terrestrial ecosystems account for approximately 6.7 Pg of carbon removal per year from the atmosphere (Fischlin et al. 2007). However, there are gaps in how the community comprehends the timing and controls on this uptake. Forests, which comprise 30% of all land surface, are some of the most productive ecosystems (responsible for roughly 2.6 Pg of carbon uptake per year), indicating that they are very effective at sequestering carbon in the form of soil organic carbon and plant biomass (Bonan 2008). But, there are underlying processes and mechanisms that control this productivity. There is a fundamental lack of understanding in the fields of ecology and biogeography as to what extent abiotic factors control to the productivity of an ecosystem and how different co-existing species might vary in their sensitivities to these factors through time.

Among the many controls on this carbon uptake, discussion of the importance of topographic aspect to the timing and distribution of carbon uptake is not well represented in the literature, despite its importance to the distribution of biodiversity (Coblentz and Riitters 2004).

Objectives

In this study, we attempt to establish a baseline understanding of the relationships between topographic aspect, hydrologic inputs, and ecophysiological activity. We sought to accomplish this by relating the abiotic conditions throughout a year to rates of atmospheric CO₂ uptake (A_{net}) and H₂O release (net transpiration) via the soil-plant-atmosphere continuum. These metrics provide a strong measure of overall plant function and response to environmental drivers.

With this information, we can then assess how significant particular environmental conditions are to future productivity.

To understand these relationships, we specifically sought to address four questions:

1. To what extent do the seasonal trends in atmospheric and soil conditions influence or control plant physiological behavior at this site?
2. Do the three co-dominating species at this site respond differently to these abiotic conditions?
3. Is there a pronounced topographic aspect effect on physiological behavior?
4. Are there interacting relationships between the season, species, and aspect effects?

PRESENT STUDY

Study Site

We conducted this study at the Mt. Bigelow site, one of four Critical Zone Observatory (CZO) research areas in the Santa Catalina Mountains just north of Tucson, AZ (These sites are part of the larger Santa Catalina Mountains and Jemez River Basin CZO). This site, located at 32° 25' 00" N, 110° 43' 31" W and approximately 2550 m in elevation, is near the second tallest peak in the Santa Catalina Mountains, which is one range of many that form the Madrean Sky Island Archipelago. These sky islands – ranges of tall mountain peaks that are geographically isolated from each other by low-elevation desert floor – are highly biodiverse regions due to both geology and climate (Whittaker and Niering 1975).

The Mt. Bigelow site is characterized by complex mountainous terrain with thin, poorly developed soils approximately 1m deep. A predominant feature of this site is a clearly defined zero-order basin (ZOB), an area on the landscape in which the only input of water is from precipitation. The ZOB is 1.5 ha and drains to the east, with opposing north- and south-facing topographic aspects of roughly equal area. The north aspect is offset 28° from geographic north and has a slope of approximately 14°; the south aspect is offset 158° from geographic north and has a slope of approximately 16°. The catchment is co-dominated by Douglas Fir (*Pseudotsuga menziesii*), Ponderosa Pine (*Pinus ponderosa*), and Southwestern White Pine (*Pinus strobiformis*), with an average canopy height of 17.3 m. While Southwestern White Pine has a relatively small global distribution, both Ponderosa Pine and Douglas Fir are found across the North American continent and are important crops in the US forestry industry (Fulé et al. 1997).

One unique characteristic of this site relative to other North American montane forests is the influence of the North American Monsoon (NAM). Due to low average annual rainfall of 690-940 mm (Brown-Mitic et al. 2007; Potts et al. 2017), this region is considered a semiarid forest. However, a majority of this precipitation falls during intense summer convective storms and the rest as winter snowfall, giving the site a bi-modal annual precipitation pattern.

Methods

Assessing primary productivity on the hectare-scale required higher spatial resolution measurements than are commonly available at the Mt. Bigelow site. While Critical Zone Observatory investigators continue to monitor ecosystem variables in the ZOB (surrounding the existing eddy covariance tower), these measurements do not capture the physiological activity that is necessary to answer the questions proposed here. Measurements of CO₂ and water vapor exchange (photosynthesis and transpiration, respectively) at the leaf-level are commonly used to capture the capability of plants to respond to environmental drivers since these drivers can be controlled very closely (Huxman et al. 2003). Thus, to determine any difference in the productivity of these species between opposing aspects, this more direct approach was used rather than existing ongoing measurements.

To accomplish the goals of this study, leaf-level measurements of plant activity were conducted for the three co-dominant species at this elevation. We chose five replicates of each species – a sample size determined based on previous literature (Gong et al. 2008; Barron-Gafford et al. 2017) (Figure 3) – and measurements were taken from the north and south aspects concurrently. This scheme resulted in 30 total samples measured each field campaign. Due to the

physical constraints of measuring within the canopy, samples were cut from individual trees and measured on the ground. To maintain hydraulic conductivity, cut branches were placed in buckets of water and re-cut underwater (Huxman et al. 2003). Once sampled branches were allowed to acclimate to ambient conditions, we took measurements of net CO₂ assimilation and transpiration using portable photosynthesis analyzers (LI-6400XT, Li-Cor, Lincoln, NE, USA) configured with light sources (model 6400-18A). The sample cuvette light intensity was set to 1500 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (to represent full daytime quantum flux), vapor pressure deficit was maintained between 1-2 kPa, and measurements were made at ambient air temperature. Following the measurements, we removed needles from inside the cuvette, detached from the stem, placed in re-sealable plastic bags, and stored on ice. We then returned those needles to the laboratory and measured total leaf area with a leaf area meter (3100-C, Li-Cor, Lincoln, NE, USA). These direct measurements provided a value of net photosynthesis and water use efficiency for individual trees that were compared amongst other samples. We coupled with each measurement of gas exchange with a measurement of the midday water potential for the same branch (Model 600, PMS Instrument Company, Albany, OR, USA), providing a value of the relative ease of water movement within the soil-leaf-atmosphere continuum. Excluding winter, we also measured pre-dawn water potentials for similar branches the night before daytime leaf-level measurements were taken.

In addition to seasonal plant physiology measurements, we also established a characterization of the stand, including species composition, diameter at breast height (DBH), and total height for a stratified random sample of 8 plots within the ZOB, as well as DBH and total height for all 30 individuals sampled. Sampled tree cores of several additional trees in the

ZOB (J. Minor, pers. comm.; Potts et al. 2017) provided ancillary information about the stand: individual age and growth patterns being the most relevant to this study.

Abiotic and environmental variables in the ZOB were measured continuously throughout the study period. Atmospheric measurements provided the following variables at a half-hour resolution: air temperature, relative humidity, and vapor pressure deficit at 1.50, 8.75, 16.00, 24.00, and 31.00 m (HMP-60, Vaisala, Helsinki, Finland), precipitation below and above the canopy (TR-525M, Texas Electronics, Dallas, TX, USA), and above-canopy net radiation (CNR-4, Kipp & Zonen, Delft, The Netherlands). Measures of soil conditions were also provided at half-hour resolution by sensors installed on both the north and south aspects: soil matrix water potential at 10 and 30 cm below the soil surface (MPS-6, Decagon Devices, Pullman, WA, USA), and soil temperature and volumetric water content at 10, 30, and 60 cm below the soil surface (5TE, Decagon Devices, Pullman, WA, USA). Below-canopy radiation was measured at 1 m above the soil surface on both north and south aspects; measurements included incoming short- and long-wave, outgoing short- and long-wave, and net radiation (CNR-4, Kipp & Zonen, Delft, The Netherlands).

Data from this project were analyzed using both the R statistical computing language and SPSS for some analyses. Time series measurements from installed sensors with half-hour resolution were generally summed or averaged to give daily representations of environmental conditions. Some of these data (incoming shortwave radiation and volumetric water content) were still quite noisy at daily time steps, so these series were further smoothed using a 5-day moving average. Plant physiological data were analyzed using a repeated measures ANOVA with Tukey's HSD post-hoc tests.

Results and Discussion

Cumulative precipitation during the study period of February 2016 through January 2017 was 651.5 mm. Figure 3 in Appendix A shows the annual distribution of temperature at the site, along with below-canopy incoming solar radiation and volumetric water content on both north and south aspects. Seasonal progression of temperature, precipitation, and relative humidity closely follow patterns observed in previous data from this site (Brown-Mitic et al. 2007; Potts et al. 2017). A clear north versus south divergence in volumetric water content emerges immediately following the end of snowmelt on the north aspect on February 20, 2016 and continues through to the dry summer season. Due to more direct insolation at the soil surface on the south aspect, a greater magnitude of soil moisture is lost to evaporation, leaving less available for root uptake (Hinckley et al. 2014).

Plant physiological activity strongly reflected these seasonal changes. Figure 1 in Appendix B (Additional Figures) presents the pre-dawn water potential (Ψ_{pd}) measurements for *P. menziesii*, *P. ponderosa*, and *P. strobiformis*, where a clear relationship can be seen between season and Ψ_{pd} ($F_{3, 15} = 27.026$; $p < 0.05$). Additionally, a strongly significant difference in Ψ_{pd} emerged between the pre-monsoon dry summer and the monsoon summer periods for all individuals (two-sided $t = -8.03$, $p < 0.0001$). A_{net} in these species was also highly dependent on this seasonal weather effect ($F_{4, 88} = 35.62$; $p < 0.0001$; Figure 2, Appendix B). Spring A_{net} was generally high, averaging $6.4 \pm 3.2 \mu\text{mol m}^{-2} \text{s}^{-1}$, and pre-dawn water potential was favorable for these individuals, averaging only $-0.9 \pm 0.2 \text{ MPa}$. Rates of A_{net} were suppressed in the dry summer ($3.8 \pm 2.0 \mu\text{mol m}^{-2} \text{s}^{-1}$); once precipitation began in the monsoon summer season, A_{net} rates rebounded to an average of $6.1 \pm 2.1 \mu\text{mol m}^{-2} \text{s}^{-1}$. Rates of A_{net} in the fall were similar to those in the spring, averaging $7.2 \pm 3.2 \mu\text{mol m}^{-2} \text{s}^{-1}$. Winter measurements of A_{net} were extremely low

($0.5 \pm 1.1 \mu\text{mol m}^{-2} \text{s}^{-1}$), with seven of 30 measurements falling below 0 (indicating net carbon release).

Some of the variation around the seasonal means of A_{net} that we detected between seasons can be correlated with differences among species. We found a significant species-by-season interaction ($F_{8, 88} = 3.96$; $p < 0.001$), indicating differences in how each species responded to the environmental characteristics of each season. Aside from the winter – when all species had very low fluxes – *P. menziesii* had very little response to seasonal changes, whereas *P. ponderosa* and *P. strobiformis* were more dynamic in their responses to environmental variation relative to *P. menziesii*.

A different way to approach our understanding of A_{net} through time is to examine carbon fluxes through the lens of a topographic aspect effect in combination with a species effect. In Figure 2, it is clear that there is very little difference between measurements of A_{net} on both aspects, and the aspect-by-season interaction effect is not significant ($F_{4, 88} = 1.96$; $p = 0.11$) for summer (dry and monsoon), fall, and winter seasons. During the spring season, we found evidence of an aspect-by-season interaction when comparing A_{net} on both aspects in spring (one-sided $t = 2.089$, $p < 0.05$; Figure 6). Though this test was significant, we further tested this effect by separating *P. menziesii* from both *Pinus* species, *P. menziesii*. The result was that *P. menziesii* was insensitive to any aspect effect (two-sided $t = 0.541$, $p = 0.604$), while rates of A_{net} within the *Pinus* species were significantly greater on the north versus the south aspect during the spring (one-sided $t = 2.469$, $p = 0.013$).

Conclusions

The results of this study indicate the importance of not only season and species to overall ecosystem-level biogeochemical cycling, but also topographic aspect. With projected changes to the climate and their potentially detrimental effects on western United States forests (Breshears et al. 2005; Adams et al. 2009), it is critical to understand and be able to model current sub-landscape-level ecosystem processes. Though only a fraction of the year, individuals of both *Pinus* species on the north aspect outperformed those on the south aspect during the spring snowmelt season. On the contrary, *P. mezesii* individuals remained relatively unaffected by soil moisture differences across aspects. Aspect-mediated advantages or disadvantages to primary productivity for species in these forests may be further exaggerated by changes to climate, with individuals on equatorial-facing aspects somewhat shielded from effects on water availability in the near-surface (Hinckley et al. 2014). Due to the importance of snowmelt for year-round montane forest productivity (Monson et al. 2005), this exaggerated difference across aspects may impair *Pinus* species from continuing to thrive on pole-facing aspects into the future. The consequences of this, based on our data, would potentially lead to lower overall productivity at the landscape-level.

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APPENDIX A

Patterns of Primary Productivity in a Mixed Conifer Forest with Complex Terrain

Patrick C. Murphy, Dan L. Potts, Kevin J. Anchukaitis, David J. P. Moore, Greg A. Barron-Gafford

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Abstract

Forests in North America are important ecosystems for carbon uptake from the atmosphere and storage within the biosphere and lithosphere. Abiotic drivers strongly influence these forests' ability to exchange water for carbon dioxide. There remain many unknowns in the extent to which local topography controls photosynthetic carbon assimilation (A_{net}) at the landscape scale. Though landscape-level net ecosystem exchange data is collected at many sites across the continent, these data products are generally insensitive to variability within the study footprint. As a result, the effect of topographic aspect on primary productivity in these forests is largely unknown. This study provides empirical data that demonstrates that differences in abiotic conditions across opposing north and south aspects drives a divergence in A_{net} . Measurements of A_{net} and net transpiration were taken on two native species (Ponderosa Pine and Douglas Fir) across two aspects at five points throughout the year. Results indicate that Douglas Fir had no apparent response to aspect. However, Ponderosa Pine increased A_{net} in response to delayed snow melt, and therefore greater soil moisture, on the north aspect. This difference in Ponderosa was sustained through June, and only disappeared at the onset of the North American Monsoon. This study shows that complex terrain in mountain forests leads to complexities in biogeochemical cycling across the landscape. A better understanding of how vegetation responds to environmental conditions and changes is critical to modeling current ecosystem function and projecting future change, especially for ecosystems as biologically and economically important as forests.

Introduction

Increasing global demand for forest ecosystem goods and services has led to increased attention on the sensitivity of forests to environmental variability (Breshears et al. 2011).

Worldwide, forests comprise 30% of land cover and are responsible for more than 38% of the 6.7 Pg of carbon uptake by terrestrial ecosystems each year (Fischlin et al. 2007; Bonan 2008).

Given the broad diversity of forest structure and function, predicting the influence of current and projected climate change on forest carbon cycling remains uncertain (Myneni et al. 2001).

Furthermore, forest responses to climate change will likely be shaped by climate-mediated feedbacks associated with extreme weather events, altered fire disturbance regimes and increased prevalence of forest pests and pathogens leading to shifts in forest community structure and composition (Adams et al. 2009).

Semiarid forests are a widespread and important contributor to regional carbon budgets (Grünzweig et al. 2003; Rotenberg and Yakir 2010) and the variation that dampens our ability to adequately predict global terrestrial carbon fluxes. Often, predicting the impacts of climate change on carbon cycling is further complicated by the fact that forest ecosystems can be distributed across topographically complex landscapes and may have a highly variable sensitivity to drought (Williams et al. 2010). Strong elevational gradients of moisture availability and distinctive seasonal variation in the timing, form, and amount of precipitation shape the structure and function of these forests (Pelletier et al. 2018). For example, the accumulation of winter snowpack and the timing of snowmelt strongly regulates the water cycle of semiarid montane forests (Vivoni et al. 2008). Earlier and more rapid snowmelt result in a reduction in soil moisture later in the growing season and may negatively impact forest productivity (Monson et al. 2002).

The influence of inter-seasonal variation in precipitation on forest productivity is further mediated by topographic variability such as hillslope position, slope, and aspect (Bennie et al. 2008; Pelletier et al. 2018). For instance, incoming solar radiation strikes more directly on equator-facing aspects, while opposing pole-facing aspects receive substantially less insolation given the more oblique angle of the sun (Figure 1). At the regional scale, aspect-mediated differences in incoming radiation contribute to widely-noted differences in forest community composition and elevational distribution of western North American forests (Whittaker and Niering 1965; Nemani and Running 1989; Coblenz and Riitters 2004). The same insolation patterns are also seen in landscape-scale catchments (Zou et al. 2007). Aspect-mediated shifts in forest ecosystem structure and function may reflect seasonally dynamic, species-specific physiological responses to the role of insolation in shaping site energy and water balance. For example, south aspects (in the northern hemisphere) may experience earlier, more rapid snowmelt relative to adjacent north aspects. As a result, soil on the south aspect becomes xeric earlier in the growing season, while soil on the north aspect remains mesic longer into the growing season (Figure 1; Gutiérrez-Jurado et al. 2006; Geroy et al. 2011; Hinckley et al. 2014).

The Madrean sky islands of northern Sonora and southern Arizona and New Mexico, are a series of isolated mountain ranges which span between the Colorado Plateau to the north and the Sierra Madre Occidental to the south (Brusca et al. 2013). Among the sky islands, the Santa Catalina Mountains have long been the focus of plant ecology research examining the interplay between climate and topography (Shreve 1915; Whittaker and Niering 1965; Whittaker and Niering 1975). Diverse conifer-dominated forest communities occupy the highest elevations of the Santa Catalina Mountains, including mixed-conifer stands of ponderosa pine (*Pinus ponderosa*), southwestern white pine (*Pinus strobiformis*), and Douglas-fir (*Pseudotsuga*

menziesii var. *glauca*). The diversity of Madrean sky island montane forests is in part of reflection of the region's distinctive hydroclimate. In addition to snowmelt, which dominates seasonal patterns of soil moisture availability in more northern Rocky Mountain montane forests, the hydroclimate of Madrean sky island montane forests is strongly influenced by summer convective storms associated with the North American Monsoon (NAM; Adams and Comrie 1997). This seasonal bimodal distribution of moisture shapes Madrean sky island montane forest carbon and water cycling by influencing species-specific patterns of photosynthetic phenology (Potts et al. 2017) and ecosystem CO₂ exchange (Brown-Mitic et al. 2007). Regional climate warming is predicted to alter the amount and seasonal timing of precipitation in these montane forests (Melillo et al. 2014).

The objective of this research was to better understand the role that topographic complexity plays in shaping species-specific physiological responses to seasonal variation in moisture availability (Chorover et al. 2007; Vose et al. 2011; Harpold et al. 2015). To address this objective, we characterized seasonal variation in plant water status and leaf photosynthesis of two co-dominant conifer species growing on opposed north- and south-facing aspects of an instrumented catchment in the Santa Catalina Mountains of southern Arizona. We predicted that the magnitude of slope aspect-mediated differences in plant physiological performance would vary with seasonal shifts in sun angle, air temperature, and soil moisture (Figure 1). Specifically, we predicted a strong influence of slope aspect on plant physiological performance during spring, a season characterized by mild temperatures and plant available soil moisture resulting from melting snow cover. Conversely, we predicted that when sun angles are higher, slope aspect-mediated differences in insolation and potential evaporation would be reduced and that trees growing on the opposing aspects would perform more similarly to one another (Figure 1).

Finally, to predict species-specific patterns of seasonal photosynthesis we extended the conceptual framework of Potts et al. (2017) to predict that slope aspect would influence seasonal patterns leaf photosynthesis according to species' thermal and moisture tolerances. Specifically, we predicted that under warm and dry conditions, *P. ponderosa* would maintain higher rates of leaf photosynthesis on the xeric south-facing aspect than *P. menziesii*, while *P. menziesii* would maintain greater rates of leaf photosynthesis than *P. ponderosa* on the cooler, mesic north-facing aspect.

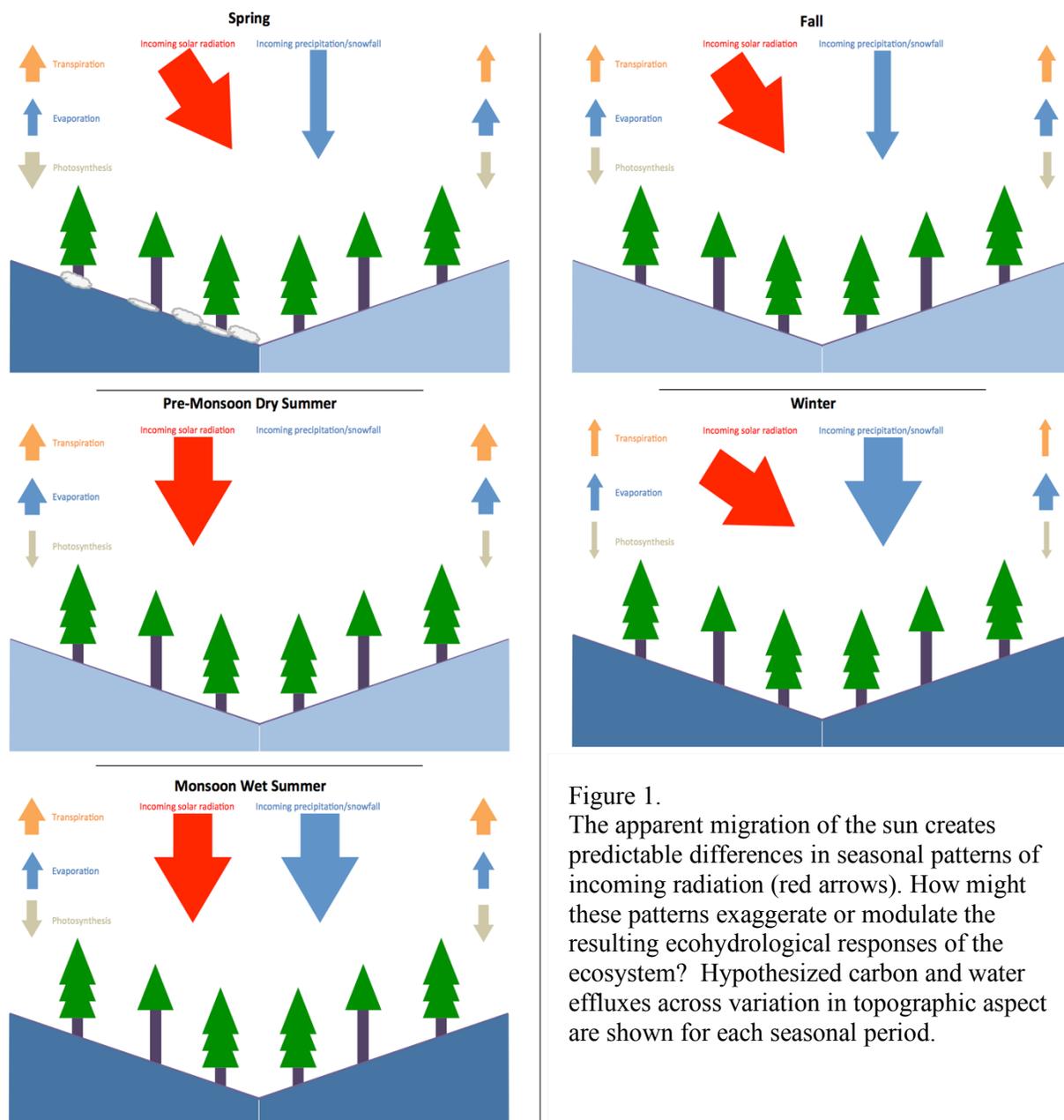


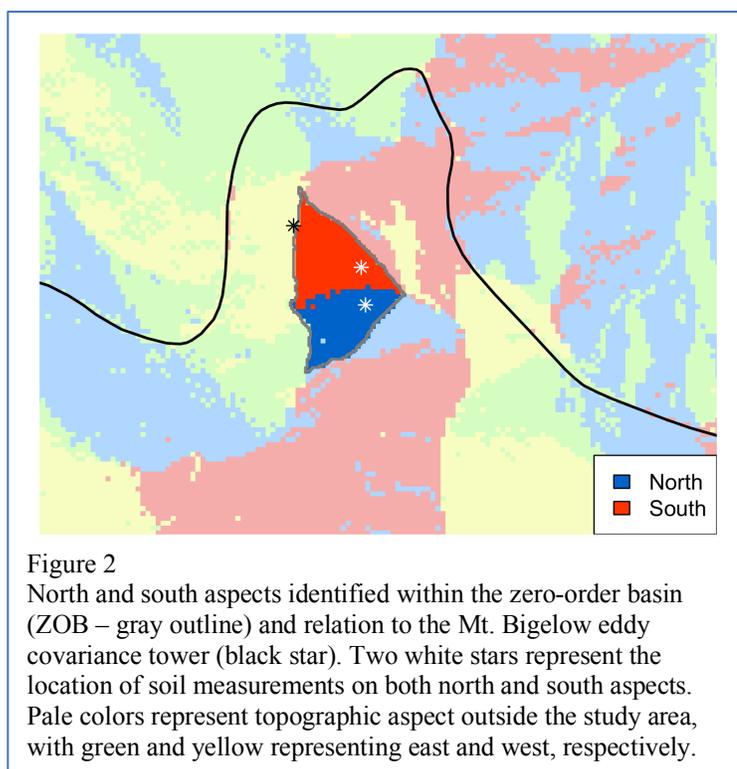
Figure 1. The apparent migration of the sun creates predictable differences in seasonal patterns of incoming radiation (red arrows). How might these patterns exaggerate or modulate the resulting ecohydrological responses of the ecosystem? Hypothesized carbon and water effluxes across variation in topographic aspect are shown for each seasonal period.

Methods

Site Description

Samples for this study were collected from the Mt. Bigelow high-elevation research site (32° 25' 00" N, 110° 43' 31" W, 2,550 m elevation), one site within the Catalina-Jemez Critical Zone Observatory. This high-elevation mixed conifer forest resides within the Coronado National Forest and experiences a semiarid, North-American Monsoon precipitation regime with annual cumulative rainfall averaging 690-940 mm (Brown-Mitic et al. 2007; Potts et al. 2017). Though individual trees are undisturbed, the United States Forest Service thinned the stand in 2009.

To address differences between individual productivity on north and south aspects, we measured photosynthetic rates of mature trees within a 1.5 ha zero-order basin (ZOB) that lies within the footprint of the Mt. Bigelow eddy covariance tower (Figure 2). This ZOB drains east, and has opposing north and south aspects with similar areas and



slopes. The north aspect is offset 28° from geographic north and has a slope of approximately 14°; the south aspect is offset 158° from geographic north and has a slope of approximately 16°. The catchment is co-dominated by Douglas Fir (*Pseudotsuga menziesii*) and Ponderosa Pine (*Pinus ponderosa*), with an average canopy height of 17.3 m. Tree-ring analyses of *P. menziesii*

within the ZOB suggest that overstory trees growing at our site established in the late 1930s (J. Minor, pers. comm.; Potts et al. 2017). See Brown-Mitic et al. (2007) for additional site information.

Environmental Data

A suite of sensors have been collecting regular measurements of above- and below-ground environmental conditions at the Mt. Bigelow site since 2009. Atmospheric measurements provided the following variables at a half-hour resolution: air temperature, relative humidity, and vapor pressure deficit at 1.50, 8.75, 16.00, 24.00, and 31.00 m (HMP-60, Vaisala, Helsinki, Finland), precipitation below and above the canopy (TR-525M, Texas Electronics, Dallas, TX, USA), and above-canopy net radiation (CNR-4, Kipp & Zonen, Delft, The Netherlands).

Measures of soil conditions were also provided at half-hour resolution by sensors installed on both the north and south aspects: soil matrix water potential at 10 and 30 cm below the soil surface (MPS-6, Decagon Devices, Pullman, WA, USA), and soil temperature and volumetric water content at 10, 30, and 60 cm below the soil surface (5TE, Decagon Devices, Pullman, WA, USA). Below-canopy radiation was measured at 1 m above the soil surface on both north and south aspects; measurements included incoming short- and long-wave, outgoing short- and long-wave, and net radiation (CNR-4, Kipp & Zonen, Delft, The Netherlands).

Plant Physiology Data

In early 2016, we identified five mature individuals from each of the three species on each north and south aspect, for a total of 30 samples. To characterize species-specific

photosynthetic phenology, we measured rates of net photosynthetic uptake across five seasonal periods of varying ambient temperature and moisture conditions (Figure 3).

Due to the physical constraints of measuring directly within the canopy, we cut samples from the canopies of individual trees to conduct our measurements on the ground. We used an extension ladder and telescoping tree pruner to collect south-facing, sun-exposed branches from mid-canopy of each individual. To maintain hydraulic conductivity, we then placed cut branches in buckets of water and re-cut them underwater, following on Huxman et al. (2003). To mitigate concerns about leaf age-mediated changes to physiological capability, we selected 1-year-old needles for these measurements.

Samples were acclimated to ambient conditions using portable photosynthesis analyzer (LI-6400XT, LI-COR, Lincoln, NE, USA) configured with LED light sources (model 6400-18A). The sample cuvette light intensity was consistently set to $1500 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (to represent full daytime quantum flux), vapor pressure deficit maintained between 1-2 kPa, and $[\text{CO}_2]$ maintained near ambient environmental concentration (400 ppm); Ambient atmospheric temperature was set to match current conditions. We monitored leaf gas exchange parameters closely to ensure that the samples within the cuvette reached stable and steady-state conditions before we logged measurements of net CO_2 assimilation (A_{net}) and transpiration. Following gas exchange measurements, we removed the needles from inside the cuvette and trimmed them such that only the needle area within the cuvette remained. We placed the needles in re-sealable plastic bags and stored them on ice. Once we returned to the laboratory, we measured the leaf area for each sample with a leaf area meter (LI-3100-C, LI-COR, Lincoln, NE, USA) as described by Fites and Teskey (1988). Finally, we corrected gas exchange measurements to account for each sample's actual photosynthetic leaf area.

We coupled each measurement of gas exchange with a measurement of the midday water potential for the same branch using a portable pressure chamber (Model 600, PMS Instrument Company, Albany, OR, USA). Pre-dawn water potential measurements (Ψ_{pd}) were also collected for each individual tree during the morning before gas exchange measurements, but separate branches were cut and removed from the same height in the canopy. Due to below freezing temperatures in the winter, branches froze before water potential measurements were collected, so no Ψ_{pd} data are available for this season.

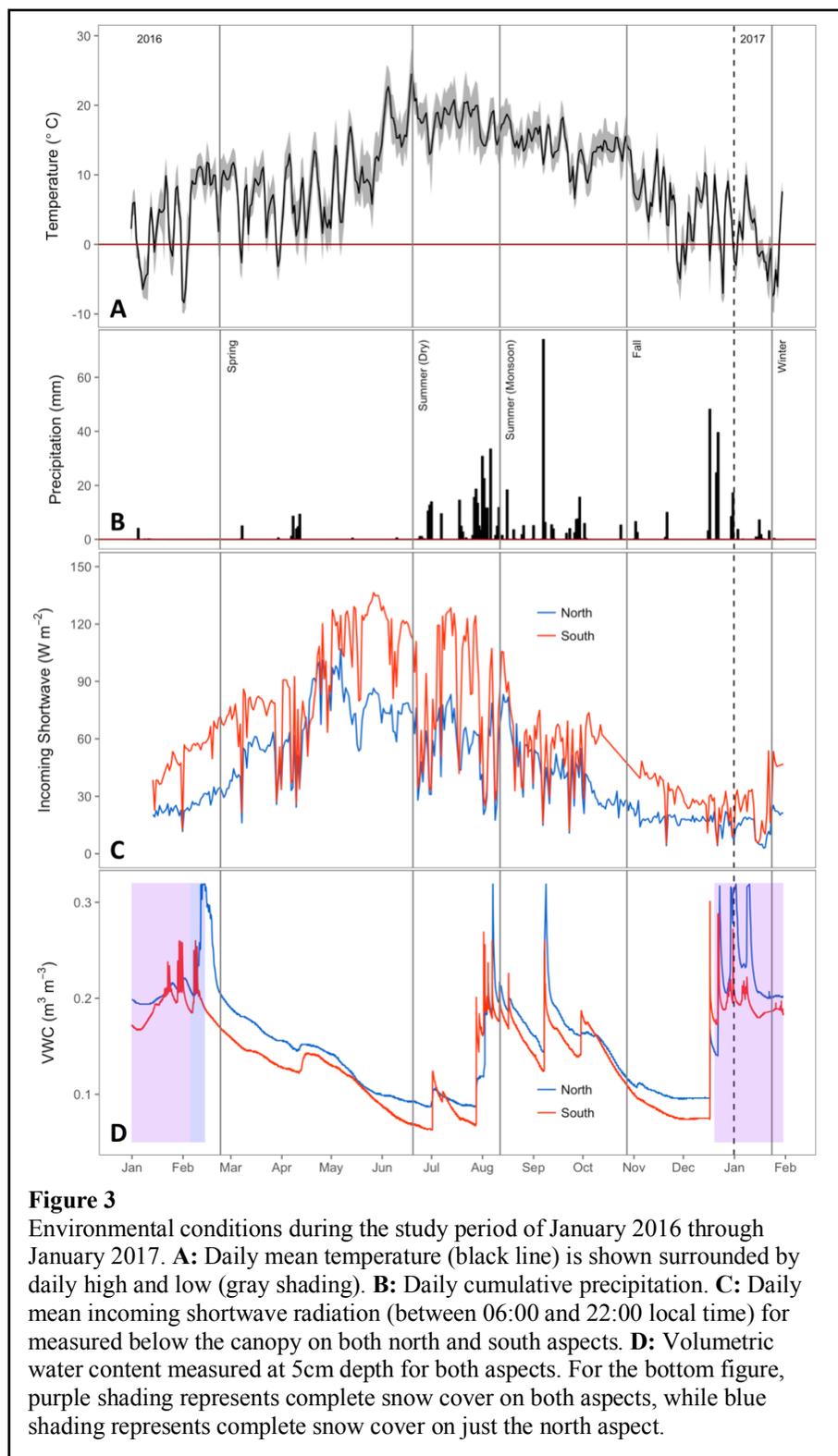
Data Analysis

Because we anticipated responses to change depending on time, we designed this as a longitudinal study. Resulting measurements of Ψ_{pd} , A_{net} , and water use efficiency were each individually analyzed as dependent variables, with season, species, and aspect included as independent variables. We assessed these groups for significance using a linear mixed effects model due to a relatively small sample size and three missing data points from the study. Significance was determined by setting a threshold of $p < 0.05$. Post-hoc tests of equal means between data subsets were done using a Tukey's HSD. Analyses were done using R 3.3.2 (R Core Team 2016).

Results

Environmental

Precipitation was unusually low throughout the first half of 2016, but increased in mid-summer at the onset of the annual North American Monsoon storms (Figure 3B). Cumulative precipitation from February 2016 through January 2017 was 651.5 mm. Air temperature and vapor pressure deficit (VPD) followed a typical annual pattern of increasing through the spring to an average of 8.2 ± 3.6 °C and 0.8 ± 0.2 kPa, respectively, and



peaking on June 18, during a period in which the average of 20.4 ± 4.3 °C and 2 ± 0.7 kPa,

respectively (Figure 3A). Temperature and VPD dropped slightly during the wet late-summer (17.0 ± 2.5 °C and 0.6 ± 0.4 kPa, respectively), and steadily declined through fall (14.4 ± 2.1 °C and 0.9 ± 0.3 kPa, respectively) and winter (-4.3 ± 2.8 °C and 0.0 ± 0.1 kPa, respectively). Belowground soil moisture and temperature varied as a result of both season and topographic aspect.

Mean annual below-canopy insolation (incoming shortwave radiation) was 66.2 % less on the north aspect due to a more oblique sun angle throughout most of the year and greater shading from the canopy at the soil surface (Figure 3C). This resulted in noticeably different timing and degree of changes in patterns of snow depth, soil moisture (Figure 3D), and soil temperature. At the beginning of the spring period in February, the north and south aspects had a snow depth of 18.3 cm and 19.6 cm, respectively. Snow cover in the ZOB began to melt first on south aspect around February 5, followed by the north aspect 9 days later. Soil moisture quickly responded to this melting snow at both the surface and a depth of 30 cm. Patterns of daytime melt are evident by the high amplitude of variation between midday and midnight soil moisture at the surface between January 18 and February 18 for the south aspect, and between February 8 and February 20 on the north. During the spring measurement period, the volumetric water content (VWC) on the north and south aspects averaged 23.7 ± 3.8 % and 17.6 ± 0.4 %, respectively.

FACTOR	DF	PRE-DAWN Ψ	A _{NET}	WUE
ASPECT	1	1.63	8.13	1.16
SEASON	4(3)	15.15	36.06	4.76
SPECIES	1	8.77	79.93	22.89
ASPECT X SEASON	4(3)	1.90	1.83	0.39
ASPECT X SPECIES	1	2.32	12.15	1.71
SEASON X SPECIES	4(3)	0.55	12.61	8.70
ASPECT X SEASON X SPECIES	4(3)	0.27	0.84	1.14

Table 1

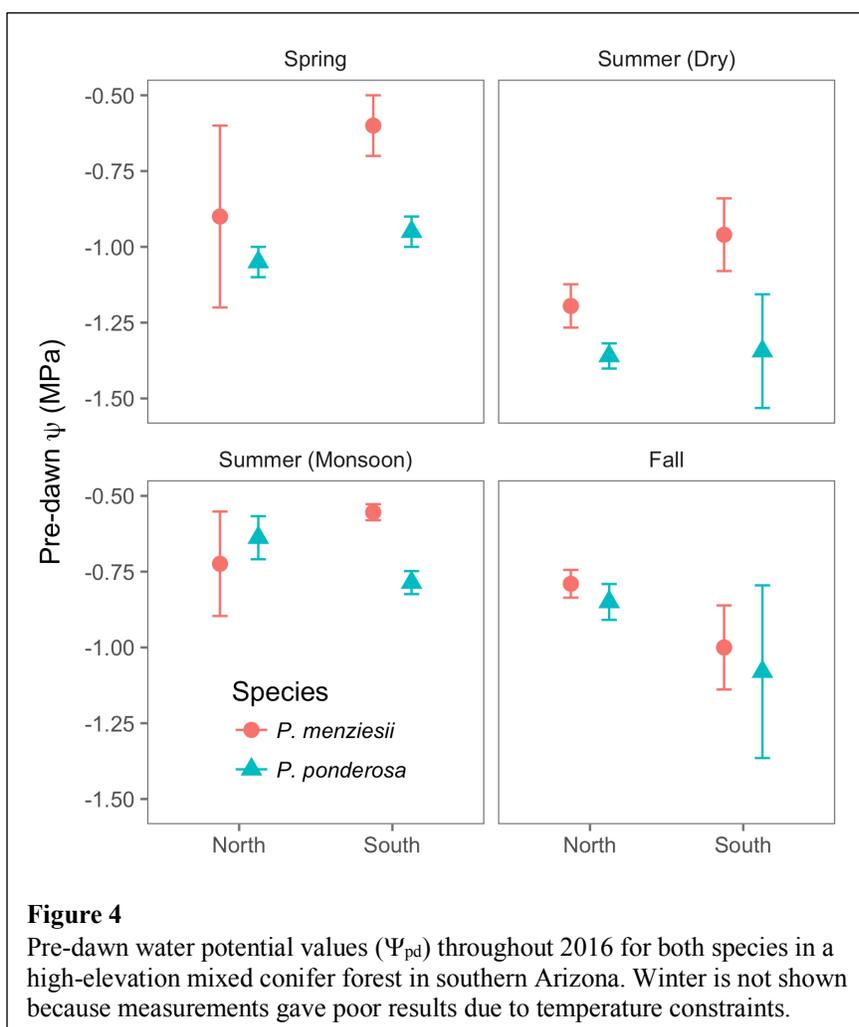
Results from linear mixed effects models of three independent variables on pre-dawn water potential, net carbon assimilation, and water use efficiency. Degrees of freedom are shown in the second column, with the first number applying to tests of A_{net} and WUE, and the number in parentheses applying to the test of Ψ_{pd} (conditions in winter prohibited collection of these data during that season). Values under each response variables are F-statistics.

Throughout late spring and early summer, differences in soil moisture between both aspects became more subtle, as soils were quite dry in mid-June with VWC at a depth of 30 cm around 9.3 ± 0.1 % and 6.9 ± 0.1 % on the north and south aspects, respectively. The first summer monsoon storm fell on July 1, with 37.1 mm of precipitation. Still, soil moisture did not rise consistently above pre-monsoon levels until August 2, after which VWC remained above 15 % on both aspects for the remainder of the summer. This transition allowed us to measure plant performance under dry summer and wet, monsoon summer conditions. While VWC responded rapidly during and immediately following rainfall, overall the soil moisture throughout the monsoon summer period (22.4 ± 6.3 % and 18.6 ± 0.9 % and on the north and south aspects, respectively) was about double the dry summer period. VWC once again steadily declined following the monsoon storms, with both aspects declining at the same rate. Values during the fall measurement period were 12.4 ± 0.5 % and 11.7 ± 0.5 % for the north and south aspects, respectively. During the winter, soil moisture remained high on both aspects due to snowmelt and occasional rain events during warmer days (20.1 ± 0.1 % and 18.7 ± 0.2 % for the north and south aspects, respectively).

Plant ecophysiology

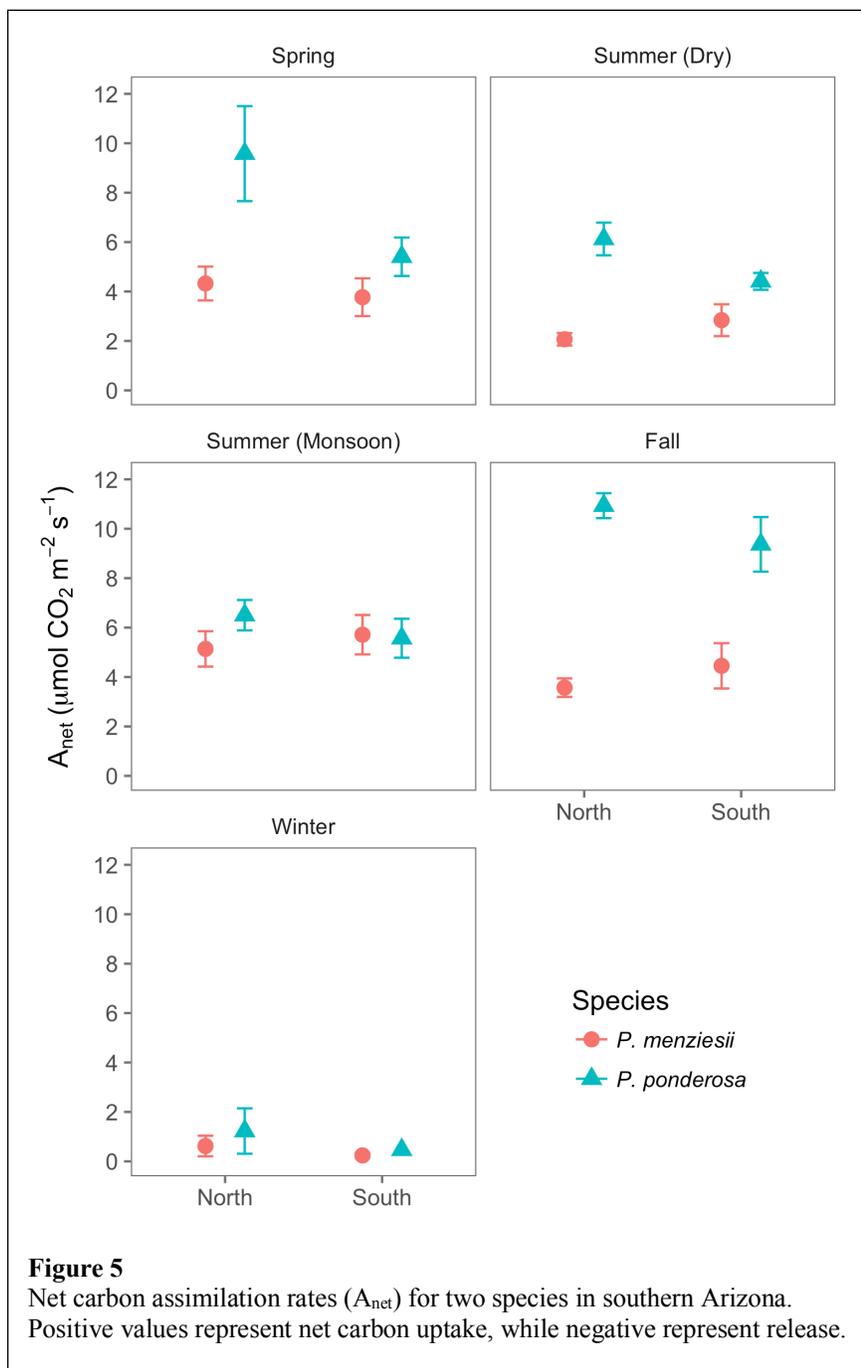
Variation in ecophysiological activity responded strongly to shifting environmental conditions, primarily as a result of seasonal change. Seasonal patterns of pre-dawn water potentials (Ψ_{pd}) for both *P. menziesii* and *P. ponderosa* followed expected patterns, with the most negative values occurring during the hot, dry early-summer season and the least negative during the late-summer monsoon season, when VWC was higher (Figure 4, Supplementary Table 1).

A_{net} for these two species was highly dependent on both seasonal and topographic patterns (Figure 5, Supplementary Table 1). Averaged across all seasons, A_{net} measurements on

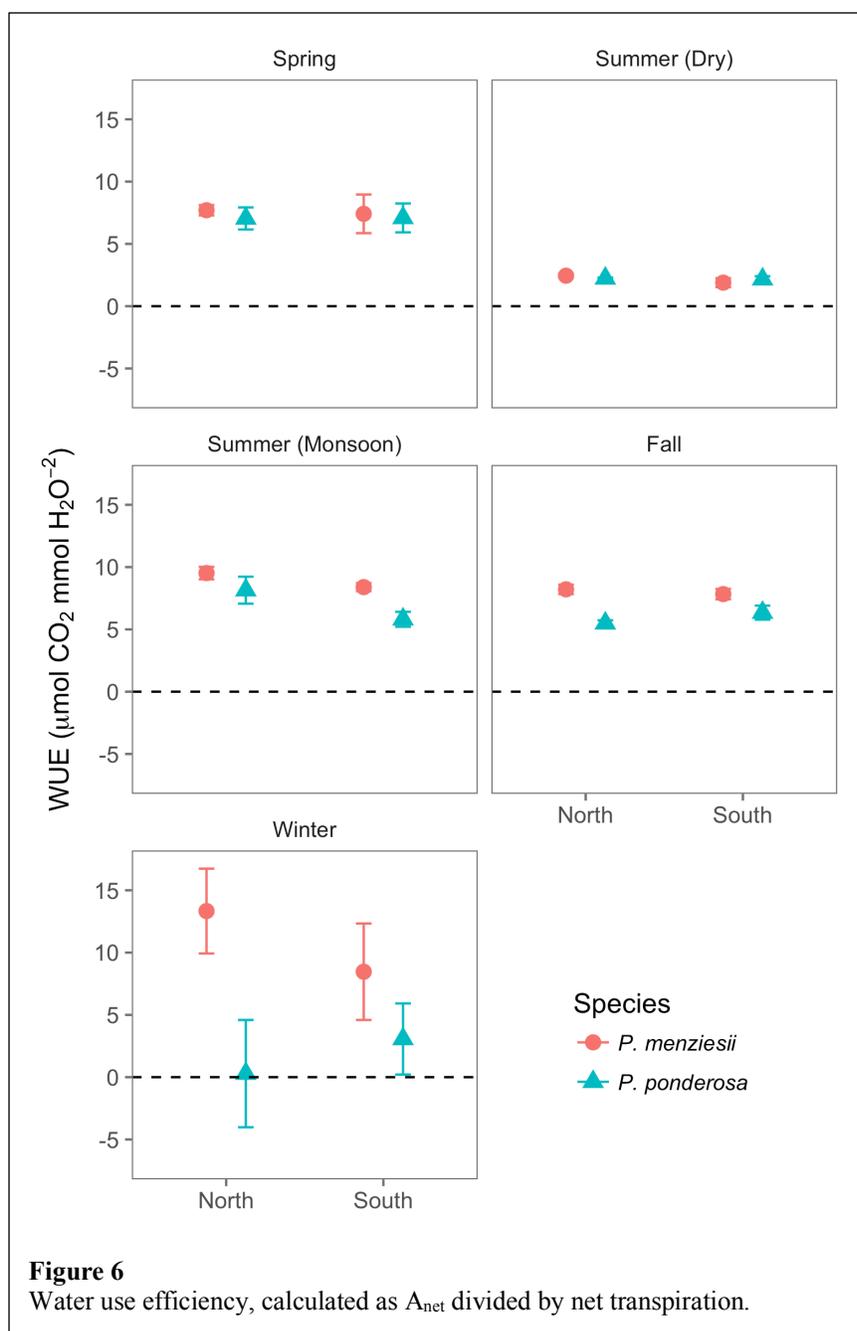


P. ponderosa were nearly 100% greater than *P. menziesii* ($6.0 \pm 0.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ versus $3.3 \pm 0.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively). Despite an insignificant F-statistic for the season-by-species-by-aspect interaction for A_{net} , post-hoc tests illustrate that there was a significant difference between measurements of *P. ponderosa* on opposing

north and south aspects during two of the five seasons studied. This indicates variation in how topography drove one species' response to seasonal changes. While topography never created discernable differences within *P. menziesii* A_{net} measurements, A_{net} did differ across aspects for *P. ponderosa* in the spring and dry summer, with indications of a trend also in the fall. In all of these cases, A_{net} was greater on the north aspect. All differences between



aspects were muted during the wet summer monsoon season and in the winter when fluxes were near zero.



Water use efficiency (WUE), calculated as $\mu\text{mol CO}_2$ assimilated per $\text{mmol H}_2\text{O}$ released, followed a seasonal pattern that closely mirrored A_{net} and net transpiration (data not shown). Relative to the spring and fall, both species dropped in their WUE during the hot and dry summer, likely because of the very low assimilation (Figure 6, Supplementary Table 1). Similarly, efficiency was very low, and even negative for some *P.*

ponderosa, during the winter. Conversely, efficiency was highest during the wet monsoon summer season. However, we found no clearly discernible difference in WUE between individuals across the opposing topographic aspects at any point during the study.

Discussion

Repeated measures of net carbon assimilation (A_{net}) on conifer trees at this site provided a greater understanding of the relationship between abiotic conditions and biotic responses. There was a strong seasonal pattern in our data resulting from the temperature and precipitation regime at the site. This seasonal effect in our data, relative to species and aspect effects, was most pronounced for pre-dawn water potential (Ψ_{pd}) and A_{net} measurements, and speaks to the environmental constraints on the dominant vegetation at this site. Both temperature and precipitation can reach extreme values depending on the season, and this imposes limitations on the ecophysiological function of these trees. Moderate temperature and water availability in spring and fall led to the highest A_{net} for both species. In both of these seasons, temperatures were generally between 10 and 20 °C, a range which includes the peak of the temperature response curve for both *P. ponderosa* and *P. menziesii* (Krueger and Ferrell 1965; Monson and Grant 1989; Huxman et al. 2003). However, A_{net} was lower in the remaining three seasons due to either temperature or precipitation constraints on primary productivity.

Here, where water availability is a common limitation on ecophysiological function, we determined that there is a clear influence of complex topography on carbon uptake and water release. Spring has been shown to be an important period of growth for montane conifer species due to favorable soil and atmospheric conditions (Monson et al. 2002). But, these soil conditions are heavily influenced by sun exposure at this semiarid site, such that equator-facing slopes may become more quickly depleted of key moisture resources (Figure 1; Hinckley et al. 2014; Pelletier et al. 2018). Measurements of A_{net} on *P. ponderosa* revealed that carbon uptake on the more mesic north (pole-facing) aspect is, on average, double that of individuals on the more xeric south (equator-facing) aspect. This can be explained by the early loss of snow cover and

rapid dry-down of plant available soil moisture on the south aspect compared to the slow, delayed melting of snow and slow dry-down on the north aspect. Lower soil moisture concentrations on the south aspect were a result of higher insolation at the soil surface, leading to quicker melt, more evaporation and sublimation, and greater water loss due to runoff (Hinckley et al. 2014). However, this same spatial pattern is not evident in the same measurements on *P. menziesii*. These individuals exhibited no response to variations in plant available soil moisture at the surface during any season. This relatively lower ‘connectivity’ between soil moisture variation and plant response is somewhat surprising since *P. menziesii* in montane ecosystems has been shown to develop shallow, fibrous roots, while *P. ponderosa* in the same ecosystem had developed deeper roots (Berndt and Gibbons 1958). If the same is true of these species at this site, this root structure would explain the physiological differences seen in Figure 5 in terms of the relative photosynthetic capacities. As a result of delayed snow melt and lower insolation on the north aspect in the spring, more of this melt water is allowed to infiltrate the soil column and saturate soils closer to the bedrock. With deeper roots, *P. ponderosa* has access to a water source that is otherwise unavailable to the shallow *P. menziesii* roots. Much less of this water is able to reach bedrock on the relatively xeric south aspect, which results in A_{net} for *P. ponderosa* that is much closer in magnitude to *P. menziesii*. *P. menziesii* carbon uptake is limited on both aspects due to rapid soil moisture loss due to evaporation.

Importantly, at no time throughout the year was *P. menziesii* more photosynthetically active than *P. ponderosa*, which is somewhat at odds to our initial hypothesis of finding higher A_{net} by these individuals on the north aspect (Figure 5). These data suggest that the more mesic conditions that would normally favor *P. menziesii* are only found at soil depths lower than these roots have access to. However, despite much lower A_{net} by *P. menziesii* individuals throughout

the year, this species' WUE rivals and sometimes exceeds that of *P. ponderosa* (Figure 6). This suggests that, while *P. menziesii* may have relatively low carbon uptake, it is able to successfully co-dominate this landscape by exchanging that carbon for very little water. WUE is quite even across both aspects throughout the year, suggesting that these species have adapted to fill their niches.

These patterns may be tied to the fact that this study site lies near the southern boundary of the *P. menziesii* distribution in North America. As such, these individuals may already be limited relative to their counterparts in more northern parts of the continent. Previous research from the state of Washington reports NPP values as high as 10-12 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for mature trees under similar conditions (McDowell et al. 2002), suggesting photosynthetic capacity for this species is dependent on latitude. Other studies have reported higher values of A_{net} for *P. menziesii* (Lewis et al. 1999; Warren et al. 2004); however, these studies have only measured seedlings, which are not entirely representative of physiological activity for mature trees. At the moment, there are too few studies on mature *P. menziesii* A_{net} to reasonably discern shifts in its photosynthetic capacity across its continental distribution.

Another consideration important to explaining these patterns is inter-annual variation – the boom and bust of patterns of C uptake across year. Unlike previous studies at this site (Brown-Mitic et al. 2007; Potts et al. 2017), our data suggests that carbon uptake remained relatively active in the dry summer period. However, inter-annual variation between our study period and that of previous data might be explained by the timing of precipitation or antecedent carry-over effects that are expressed over several seasons (Peltier et al. 2016). Similarly, a lack of winter C uptake (and in some cases, net respiration) during this study period compared to mild uptake seen in previous studies (Grünzweig et al. 2003; Brown-Mitic et al. 2007; Potts et al.

2017) can be attributed to uncommonly low winter temperatures during our study period. It has been shown that trees in these high elevation forests tend to limit or terminate photosynthetic activity during very low (below freezing) temperatures (Monson et al. 2005). These inter-annual variations can provide great insights into the plasticity of these species across potential climate scenarios.

Thinking beyond the scope of traditional ecophysiological research, this study of primary productivity across topographic aspect may also have implications for longer temporal ecosystem development. The Effective Energy and Mass Transfer model (EEMT; Rasmussen et al. 2011; Rasmussen et al. 2015), includes carbon and water fluxes through vegetation as a primary input of energy into the Critical Zone. Rasmussen et al. (2015) and Chorover et al. (2011) both report higher annual EEMT (that is, higher combined fluxes of both energy and mass) on the north aspect at several semiarid research sites in the southwestern United States, despite generally lower insolation on these pole-facing aspects throughout the year. This was hypothesized to be a function of primary productivity, rather than strictly abiotic controls on energy flux; however, empirical data was not yet available to quantify this effect on ecosystem development. This study provides a first-look of the relationship between topographic aspect, primary productivity, and ecosystem-wide patterns of soil development, hydrologic partitioning, and canopy structure.

Conclusions

A primary focus in ecosystem science is to effectively understand and describe the spatial and temporal patterns of ecosystem processes. Development of ecosystem monitoring tools and networks over the last several years have dramatically improved our ability to bound our estimates of ecosystem responses to projected climate conditions, but even these powerful data can be limited in resolution and/or coverage across space and time. As such, these measurements can be insensitive to variation resulting from community structure and topography. Current models of forest response to environmental change address landscape-wide and inter-regional behavior, but sometimes fail to capture the finer-scale processes that determine how a forest functions. With forecasted changes to climate, ecosystems – particularly those in drylands - are especially vulnerable to changes in ecosystem function (Williams et al. 2010; Williams et al. 2012). This study provides new insight into how the movement of carbon dioxide and water vapor are dependent on the interrelationships between the biotic, abiotic, and time domains.

Unlike a similar community on flat terrain, vegetation at this site is subject to additional controls such as turbulent atmospheric conditions, and differences in soil structure, soil water retention, and solar energy input (Zapata-Rios et al. 2015). Like many montane mixed conifer forests, which see high productivity during the spring months, this site had carbon assimilation rates during the snowmelt period that surpassed peak growing season rates. The importance of sustained snowpack to productivity in mountain forests is evident not only by the seasonal differences in photosynthetic uptake, but also the in the significant increase of photosynthetic uptake by *P. ponderosa* individuals growing on the mesic north aspect relative to those on the xeric south aspect. It also speaks to the potential for a loss in productivity with lower projected snowpack in western United States forests: on a very small scale, our opposing aspects in spring

behave as a mesocosm of current climate conditions versus anticipated climate conditions. In this study, snow on the north aspect remained on the ground through most of February and melted slowly, which is characteristic of montane conifer forests currently and in the past. Relative to the north, snow on the south aspect melted and sublimated more rapidly, much in the same way we would expect a snowpack to react to an earlier onset of the growing season and warmer growing season temperatures in the future. It is clear from this dataset that individuals of the genus *Pinus* growing on the north aspect in this semiarid forest are quite responsive to this delayed snowmelt relative to their counterparts on the opposing south aspects. Additionally, relative to *P. menziesii*, they are responsible for higher overall carbon uptake regardless of season or aspect. This leads to the possibility that in a future with earlier snowmelt, lower overall carbon sequestration from a *Pinus*-dominated landscape is a strong possibility. The patterns seen at this site speak to the dynamic relationship between plants and their environment, and they provide insight into possible future ecophysiological responses to changing climatic conditions.

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North aspect South aspect	Pre-dawn water potential (Ψ_{pd} , MPa)		Net assimilation (A_{net} , μ mol CO ₂ m ⁻² s ⁻¹)		Water use efficiency (WUE, μ mol CO ₂ mmol H ₂ O ⁻¹)	
	<i>P. menziesii</i>	<i>P. ponderosa</i>	<i>P. menziesii</i>	<i>P. ponderosa</i>	<i>P. menziesii</i>	<i>P. ponderosa</i>
Spring	-0.90±0.30 -0.60±0.10	-1.05±0.05 -0.95±0.05	4.3±0.7 3.8±0.8	9.6±1.9 5.4±0.8	7.7±0.4 7.4±1.6	7.0±0.9 7.1±1.2
Summer (dry)	-1.20±0.07 -0.96±0.12	-1.36±0.04 -1.34±0.19	2.1±0.3 2.8±0.6	6.1±0.7 4.4±0.3	2.4±0.2 1.9±0.4	2.2±0.1 2.2±0.2
Summer (monsoon)	-0.72±0.17 -0.55±0.03	-0.64±0.07 -0.79±0.04	5.1±0.7 5.7±0.8	6.5±0.6 5.6±0.8	9.5±0.5 8.4±0.3	8.1±1.1 5.8±0.6
Fall	-0.79±0.05 -1.00±0.14	-0.85±0.06 -1.08±0.28	3.6±0.4 4.5±0.9	10.9±0.5 9.4±1.1	8.2±0.4 7.8±0.4	5.5±0.2 6.3±0.6
Winter			0.6±0.4 0.2±0.1	1.2±0.9 0.5±0.6	13.3±3.4 8.5±3.9	0.3±4.3 3.1±2.9

Suppl. Table 1

Means and standard errors for Ψ_{pd} , A_{net} , and WUE for each season, species, and aspect (north and south on top and bottom, respectively). Winter values of Ψ_{pd} not reported due to unsuitable measurement conditions.

APPENDIX B
ADDITIONAL FIGURES

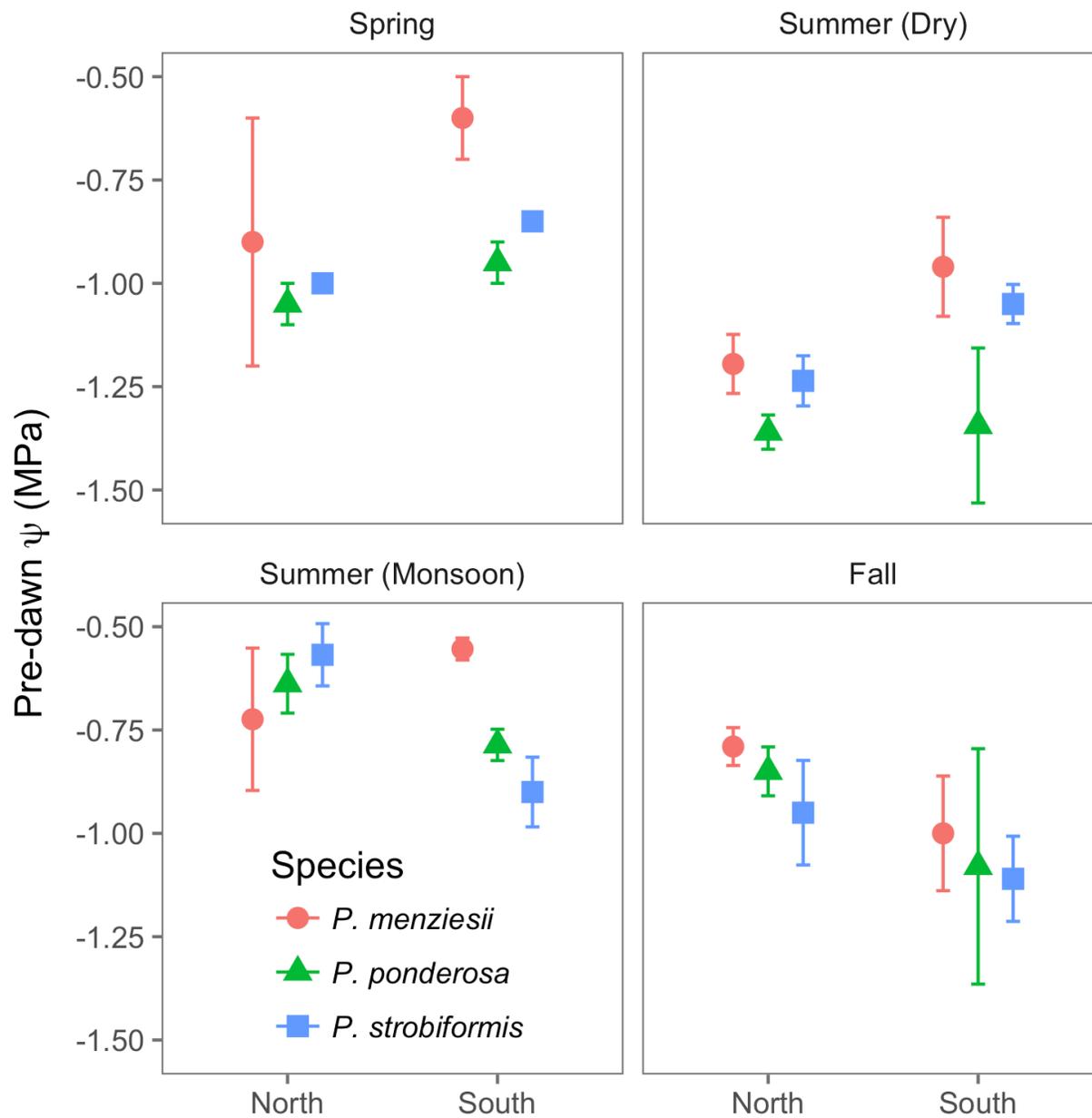


Figure 1

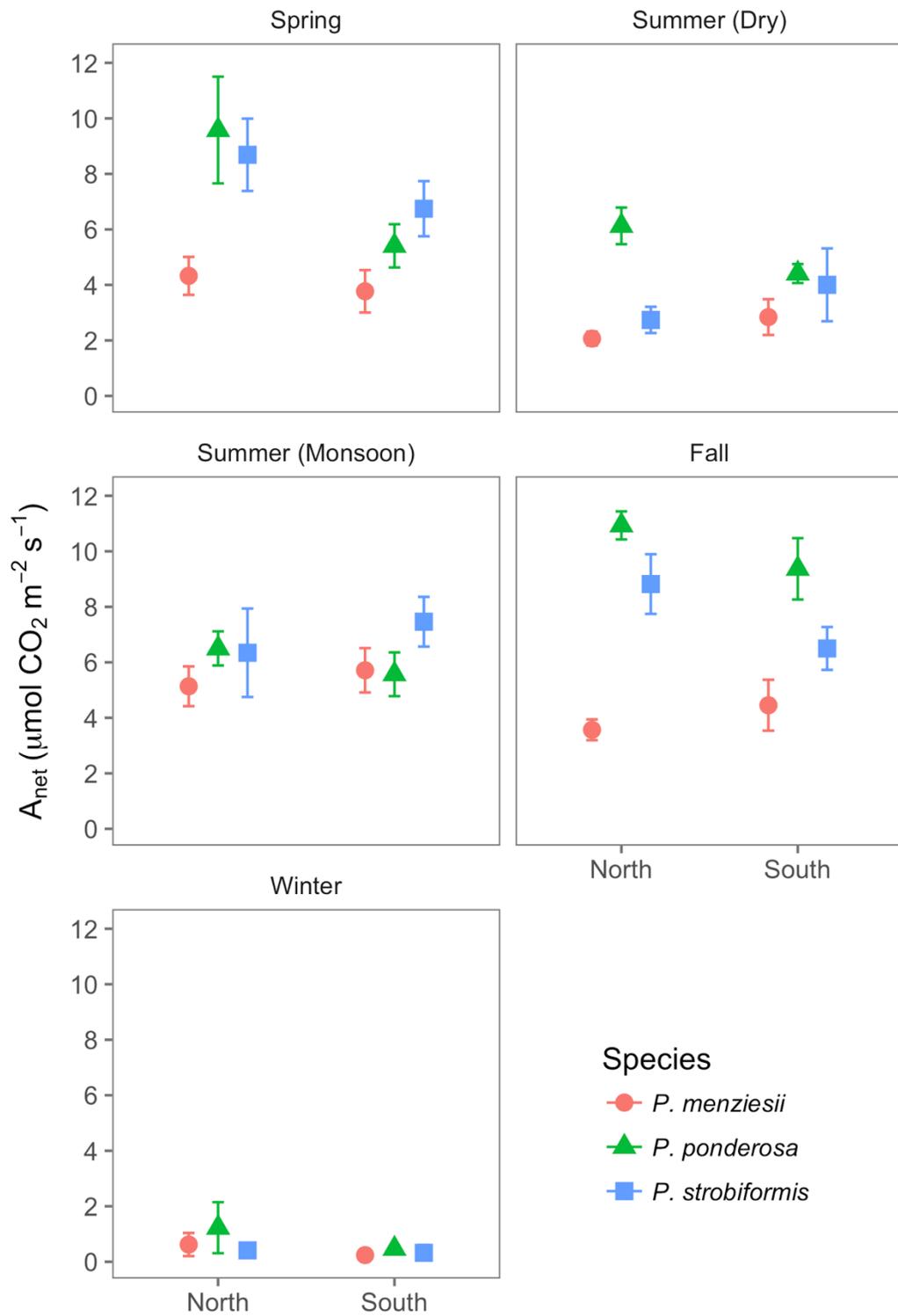


Figure 2