Temporally-varying water use strategies in *Juniperus osteosperma* mediate ecosystem carbon fluxes

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### Summary

* Some plants exhibit temporally flexible hydraulic regulation, in which the strictness of hydraulic control (i.e., iso/anisohydry) changes in response to environmental conditions. However, the environmental controls over iso/anisohydry and the implications of flexible hydraulic behavior for plant productivity remain unknown.
* In *Juniperus osteosperma*, a drought-resistant dryland conifer, we collected a 5-month growing season timeseries of *in situ*, high temporal-resolution plant water potential () and stand gross primary productivity (GPP). We quantified the stringency of hydraulic regulation associated with environmental covariates and tested the contribution of predawn water potential to modeling carbon uptake.
* *J. osteosperma* showed less stringent hydraulic regulation (toward anisohydry) and higher productivity after monsoon precipitation pulses, when soil moisture and atmospheric demand were high, which corresponded to higher GPP. The inclusion of plant water potential improved modeled estimates of GPP more strongly than the inclusion of soil and/or atmospheric moisture.
* Flexible hydraulic regulation appears to allow *J. osteosperma* to prolong soil water extraction and the period of high carbon uptake following episodic rain events during the growing season. More broadly, plant water potential and its hydraulic regulation are highly dynamic, suggesting why both process-based and empirical models often underestimate the magnitude and temporal variability of dryland GPP.

Keywords: carbon uptake, dryland ecosystem, hydraulic regulation, juniper woodland, iso/anisohydry, precipitation pulse dynamics, stem water potential

### Introduction

Along the soil-plant-atmosphere continuum, gradients of water potential () drive water transport and govern the tradeoff between obtaining carbon dioxide for photosynthesis and water loss through stomata (Berry *et al.*, 2010). The concept of a ‘plant water use strategy’ encompasses the numerous ways plants have evolved to confront this inescapable dilemma, including the popular iso/anisohydry spectrum based on the stomatal regulation of (Jones, 1998; Tardieu & Simonneau, 1998). Isohydry describes a conservative stomatal strategy to minimize reductions in and preserve hydraulic conductivity, while anisohydry is a profligate stomatal strategy that prioritizes carbon gain at the expense of low . The degree of iso/anisohydry is generally operationalized as a species-level and theoretical trait, describing a strategy in response to declining soil moisture in the absence of other limiting factors (Novick *et al.*, 2019). However, recent work has demonstrated that these strategies can be quite variable within a species and may arise from plant-environment interactions (Hochberg *et al.*, 2018), including vapor pressure deficit (VPD), which is often decoupled from soil moisture at short timescales (Novick *et al.*, 2016). Within-species shifts in iso/anisohydry have been reported for *Larrea tridentata* (Guo *et al.*, 2020) and *Quercus douglasii* (Feng *et al.*, 2019) in different seasons, in *Quercus suber* due to competition (Haberstroh *et al.*, 2022), *Acacia aptaneura* as a result of repeated experimental drought (Nolan *et al.*, 2017), and in multiple species between wet and dry years (Wu *et al.*, 2021).

The implications of temporally-variable hydraulic strategies on ecosystem carbon (C) fluxes are not yet fully understood. This knowledge gap limits our ability to model the dynamics of the land carbon sink, thereby limiting our ability to predict and mitigate climate change impacts (Kennedy *et al.*, 2019a; Novick *et al.*, 2022). Particularly in dryland ecosystems, persistent water limitation and episodic precipitation promote tight coupling between carbon and water cycles (Biederman *et al.*, 2016), resulting in added temporal complexity that can be difficult to model (Noy-Meir, 1973; Loik *et al.*, 2004; Ogle & Reynolds, 2004; Feldman *et al.*, 2018). Dryland ecosystems are largely responsible for the interannual variability of the global carbon sink (Poulter *et al.*, 2014; Ahlström *et al.*, 2015), yet dynamic global vegetation models have been found to significantly underestimate the interannual variability of C uptake in dryland regions (Biederman *et al.*, 2017; MacBean *et al.*, 2021a). Understanding the temporal dynamics and environmental sensitivity of plant hydraulic strategies may be critical to improving predictive forecasts of the global carbon cycle (Eller *et al.*, 2020; Sabot *et al.*, 2020, 2022).

Despite its importance, plant hydraulic stress is often notably absent from large-scale estimates of ecosystem productivity (Smith *et al.*, 2019). Such models commonly combine remotely-sensed indices of vegetation greenness and light use efficiency (Running *et al.*, 2004; Zeng *et al.*, 2022), defined as the slope of the relationship between biomass and cumulative intercepted photosynthetically active radiation (Monteith *et al.*, 1977). Greenness indices can represent the structural capacity for photosynthesis on a seasonal basis (Wang *et al.*, 2022), but do not capture the immediate constraints imposed by soil and atmospheric drought, such that productivity seasonality is much weaker in remotely-sensed than tower-based data in semi-arid and evergreen ecosystems (Garbulsky *et al.*, 2008; Biederman *et al.*, 2017; Smith *et al.*, 2019; Pierrat *et al.*, 2021). Instead, water stress effects are empirically incorporated into light use efficiency (LUE), which can be especially challenging to represent in dryland regions and during periods of drought (Leuning *et al.*, 2005; Zhang *et al.*, 2007), as productivity is highly sensitive to soil moisture deficits beyond what is reflected in atmospheric dryness (Novick *et al.*, 2016; Stocker *et al.*, 2018). Plant water potential, a direct metric of plant water stress that integrates soil and atmospheric drivers, may thus provide a key physiological constraint on ecosystem productivity in drylands, which could improve our ability to represent drought impacts and quantify interannual variability of C uptake.

Pinyon-juniper woodlands are broadly distributed in the southwestern United States and provide a well-studied test system for how hydraulic strategies like iso/anisohydry can modulate productivity and mortality (McDowell *et al.*, 2008). Pinyon mortality following the 2002-2003 drought was likely associated with differences in plant hydraulic regulation (Breshears *et al.*, 2009; Plaut *et al.*, 2012); juniper survival was largely attributed to a less hydraulically vulnerable xylem and thus a greater ability to withstand low water potentials (McDowell *et al.*, 2008). Although generally considered anisohydric, *Juniperus monosperma* exhibited strong stomatal control and negligible xylem embolism under drought manipulation (Garcia-Forner *et al.*, 2016b), thereby challenging the hypothesis that anisohydric species are more prone to hydraulic failure. As the southwestern US megadrought persists (Williams *et al.*, 2022) and induces mortality even among resilient *Juniperus* spp. (Kannenberg *et al.*, 2021), it is imperative to examine how flexible hydraulic strategies interact with plant productivity and survival.

In this study, we utilize a five-month time-series of plant and gross primary productivity (GPP) in a juniper woodland to evaluate the temporal dynamics of hydraulic strategy and incorporate plant water stress into a common, remotely-sensed approach to GPP. By contemporaneously measuring plant and GPP continuously at daily resolution, we can directly investigate the implications of regulation and predawn water potential for productivity in an iconic southwestern species. We ask:

1. Does plant hydraulic regulation vary over time in *J. osteosperma*?
2. What are the temporal patterns in hydraulic regulation and GPP over a growing season?
3. Can GPP prediction be enhanced by plant water potential?

### Materials and Methods

This study was conducted at an early-successional pinyon-juniper woodland (37.5241 N, 109.7471 W, 1866 m a.s.l.) in southeastern Utah. Local climate conditions include cold winters and hot, dry summers, with high interannual variability in summer precipitation due to its location at the northern boundary of the North American Monsoon. The locally flat topography is dominated by Utah juniper (*Juniperus osteosperma*, 92% tree basal area) and two-needle pinyon (*Pinus edulis*, 8% tree basal area), with sparse understory comprising big sagebrush (*Artemisia tridentata*), prickly pear cactus (*Opuntia* spp.), and bunchgrasses. See Kannenberg et al. (2023) for further site details.

#### Eddy covariance and environmental variables

An eddy covariance flux tower (AmeriFlux US-CdM) was deployed in June 2019 to measure fluxes of water, carbon, and energy and to monitor site-level meteorological and soil variables (Kannenberg *et al.*, 2022a). The sonic anemometer (Campbell Scientific CSAT3), open-path infrared gas analyzer (Campbell Scientific EC150), and temperature/relative humidity sensor (Vaisala HMP155) were installed at a height of 8 m, while the net radiometer (Kipp and Zonen CNR4) and photosynthetic photon flux density sensor (Kipp and Zonen PQS1) were installed at a height of 6.45 m. Site precipitation was measured with a tipping bucket rain gauge (Campbell Scientific TE535WS), while volumetric water content and soil temperature were monitored with five sensors (Acclima TDT) deployed at depths of 5 cm, 10 cm, 20 cm, 50 cm, and 100 cm. See Kannenberg et al. in revision for additional details on calibration and maintenance.

Eddy covariance and environmental data were processed first by summarizing to half-hourly values, gapfilling, and then summarizing to daily values used in the subsequent figures and analysis. High frequency eddy covariance data were processed into half-hourly values of net ecosystem exchange (NEE) using *EasyFlux PC* (Campbell Scientific) following a procedure of despiking (Vickers & Mahrt, 1997), coordinate rotation, spectral correction (Massman, 2000), and Webb-Pearman-Leuning density correction (Webb *et al.*, 1980). NEE was gap-filled using the 50th percentile Ustar distribution and partitioned into GPP and ecosystem respiration using the nighttime method (Reichstein *et al.*, 2005) in the R package ‘REddyProc’ (Wutzler *et al.*, 2018). All environmental variables were aggregated to 30 minute temporal resolutions; air temperature, vapor pressure deficit, and incoming shortwave radiation were gap-filled using the MDS algorithm (Reichstein *et al.*, 2005). Ecosystem fluxes and precipitation were aggregated to daily sums, vapor pressure deficit was summarized to daily maximums, and the remaining environmental variables were summarized as daily means.

#### Plant water potential

Stem water potential of seven mature *J. osteosperma* within the tower footprint (< 20 m) was monitored with both automated and manual measurements between May 24 and November 5, 2021. Half-hourly water potential was monitored with stem psychrometers (ICT International PSY1) calibrated prior to installation. Two instruments per tree were installed by removing the bark and phloem to expose a flat xylem surface. Psychrometer sensor heads were attached with self-adhesive silicone tape to maintain a tight seal and wrapped in reflective insulation to minimize temperature gradients. Because plant wounding responses can fill the sensor chamber, each psychrometer was uninstalled, cleaned with chloroform, and reinstalled on a new branch every 4-5 weeks. The day after reinstallation, the xylem water potential was measured manually with a Scholander-type pressure chamber (PMS 610) by excising a needle cluster with diameter between 2 and 4 mm and measuring within 2 minutes of collection; psychrometer water potentials generally matched pressure chamber values (Kannenberg *et al.*, 2023).

The half-hourly stem water potential time series were subjected to quality control by visual assessment and processed to daily values. After removing data during the maintenance period (+ 1 day) and outliers that were > 0.5 MPa from adjacent points, data that met the following criteria were also discarded: 1) a step change in the magnitude of water potential not attributable to a precipitation event; 2) loss of diurnal pattern in water potential. On average, data from 10 out of 14 psychrometers were available during a given period. Half-hourly stem water potential was summarized to predawn (, 2 hours prior to sunrise) and midday (, 2 hours following solar noon) for each logger. In addition, site-level means of predawn and midday water potential were calculated and missing values (10 and 8, respectively) were imputed using Kalman Smoothing via the R package ‘imputeTS’ (Moritz & Bartz-Beielstein, 2017).

#### Vegetation indices and fAPAR

Following a Monteith light use efficiency (LUE) framework (Monteith, 1972), we used the near-infrared reflectance of vegetation index (NIRv) to represent the fraction of photosynthetically active radiation absorbed by the vegetation (fAPAR) – the key proxy of the structural capacity for photosyntehsis on a seasonal basis (Badgley *et al.*, 2017, 2019). We calcluated NIRv from Moderate Resolution Imaging Spectroradiometer (MODIS) nadir bidirectional reflectance distribution function (BRDF) adjusted daily reflectance product (MCD43A, 1 d, 500 m, collection 6.1). MODIS bands 1 (620-670 nm) and 2 (841-876 nm) were combined with background soil reflectance of 0.08 to represent NIRv following Badgley et al. (2017). For each day of the measurement period, we selected all pixels within a \_\_ radius of the site (\_\_ total pixels) to roughly match the footprint of the flux tower. We then filtered these pixels to include only the highest quality observations (MODIS quality flag = 0). Resulting values were smoothed using a Savitzky-Golay filter of derivative order 0, filter order 3, and window length 5. NIRv is well-correlated with modeled fAPAR across all soil reflectances and is robust at low vegetation cover (Badgley *et al.*, 2017; Wang *et al.*, 2022). Following Monteith, incoming PAR (from the tower-mounted sensor) and NIRv were evaluated as the primary drivers of GPP (see Section 0.3.5).

#### Model description - hydraulic regulation

To specify the hydraulic regulation model, we used the Martinez-Vilalta et al. (2014) equation to relate to :

where represents the stringency of hydraulic regulation and describes the pressure drop when soil moisture is not limiting. Plant hydraulic regulation can be described as isohydry if , anisohydry if , and extreme anisohydry if .

To allow hydraulic regulation and GPP to vary over the growing season, we specified a hierarchical Bayesian model that estimated and as linear functions of maximum daily vapor pressure deficit () and volumetric soil water content at 10 cm (), which had the highest correlation with plant and GPP (Kannenberg *et al.*, 2023). Furthermore, we implemented the stochastic antecedent model (Ogle *et al.*, 2015) to quantify the influence of past environmental conditions. The data model for hydraulic regulation describes the likelihood of each observed , which was normally distributed for each observation ():

where is the predicted or mean midday water potential and represents the observation variance. was modeled according to Eqn. 2, where all terms were allowed to vary over time, either as direct observations (,) or as modeled parameters (, ). The time-varying estimates of hydraulic regulation, and were indexed by and modeled as linear combinations of two antecedent covariates and their interaction:

The and parameters were estimated for all trees. and represent the random effects of each tree, where indicates tree associated with each observation . and were scaled using the 2021 mean and standard deviation so that regression coefficients could be compared and and could be interpreted as and , respectively, under mean environmental conditions. Antecedent variables (Ogle *et al.*, 2015) were constructed using daily time series of each scaled environmental variable:

where indicates the time step, represents the total number of past time-steps considered, and indicates the weight or relative importance of the th time step into the past, and and are the observed value of each variable at time steps ago. Antecedent covariates are weighted averages of past covariate values, where the weights are stochastically determined by the data. In this analysis, was constructed using daily values from the current day to 4 days ago ( = 1, = 5), while was constructed using three-day averages of from the current day to 20 days ago ( = 3, = 7).

In order to complete this model, a zero-centered hierarchical normal prior was specified for tree random effects:

where reparameterization by sweeping was employed to ensure identifiability between the intercepts (, ) and the random effects (Vines *et al.*, 1996).

All remaining parameters were given standard priors following Gelman et al. (2014). The regression coefficients were assigned relatively non-informative normal priors centered at zero with large variance. Antecedent importance weights, vectors of length (Eqn. 4), were given non-informative Dirichlet priors that assume *a priori* that each past time step has equal importance, and that constrain weights for each covariate to sum to 1 across all time steps, . The standard deviation of tree random effects ( and ) were given relatively non-informative priors, while the measurement error precision () was assigned a conjugate, relatively non-informative prior.

#### Model description - GPP

To assess the drivers of daily ecosystem productivity, we developed a two-part model based on the Monteith (1972) framework. Daily GPP was sequentially modeled as a function of the structural capacity for photosynthesis (NIRv) and incoming PAR; the residuals were interpreted as LUE and evaluated as combinations of water stress indices, including soil moisture, VPD, and predawn water potential.

The likelihood of observed was normally distributed for for each observation ():

where is the predicted or mean daily GPP and the variance represents the uncertainty in observed . was modeled as a linear function of NIRv, PAR, and their interaction, representing the initial component of the Monteith (1972) formulation **?@eq-monteith**.

All remaining parameters were given standard priors as previously described.

To express the remaining effects of after is accounted for, we calculated the residuals of the above model as the posterior mean of ; residuals were scaled for improved model mixing. The likelihood of the residual model described scaled as normally distributed for observations ():

where is the predicted residual between observed and modeled (Eqn. 6, Eqn. 7) GPP, and the variance represents the uncertainty in observed . is interpreted as a dynamic constraint on the relationship. We devised three formulations that account for the combined impact of concurrent VPD and antecedent soil moisture (Eqn. 9), antecedent soil moisture alone (Eqn. 10), and concurrent predawn water potential (Eqn. 11):

where were the gapfilled means of predawn water potential at the site level. Antecedents weights for were constructed identically to Eqn. 4, with unique weights determined by the GPP residuals.

#### Model implementation and interpretation

The above models were implemented in JAGS 4.3.0 (Plummer, 2003) using R 4.1.1 and ‘rjags’ 4.13 (R Core Team, 2021; Plummer, 2022). For each model, three parallel Markov chain Monte Carlo sequences were initiated with dispersed starting values; initial iterations were run until model convergence, as indicated by the Gelman and Rubin (Gelman & Rubin, 1992) statistic. Models were then run for 150,000 iterations and thinned by 50 to reduce within-chain autocorrelation and storage requirements, yielding a total of 9000 relatively independent posterior samples for each quantity of interest, including the regression coefficients and antecedent weights. Posterior distributions were summarized by their means and 95% highest posterior density credible intervals (henceforth, 95% CIs). Covariate effects were significant if the 95% CI did not overlap zero. To quantify seasonal variation in , the posterior samples of the regression coefficients and antecedent weights were combined with the time-series of scaled and to produce posterior means and 95% CIs. Model comparison criteria for the three forms of GPP residual models included posterior predictive loss (Gelfand & Ghosh, 1998) and the coefficient of determination () between observed and predicted values.

### Results

#### Seasonal dynamics of , GPP, and

Over the study period, predawn () and midday () stem water potentials responded dynamically to moisture inputs, particularly during the monsoon period (Fig. 1, Fig. 2 a). Monsoon onset was determined as the day on which on the 10% of the total July, August, and September precipitation was accumulated (Grantz *et al.*, 2007), which was achieved on 2021-07-23. Prior to monsoon onset, the generally high vapor pressure deficit (D) and low volumetric water content (W) yielded relatively consistent mean between -2 and -4 MPa. During the monsoon period, D and W were less extreme than during the more arid mid-summer period, though highly variable as a result of three major pulse-drydown events (Fig. 1). Beginning with the first major pulse event (39 mm on 2021-07-27), mean remained above -2 MPa continuously for 46 days; however, minimum mean was similar in premonsoon and monsoon periods due to rapid decline in following the third major pulse-drydown. Finally, mean stayed above -2 MPa during the fall season, likely due to cooling temperatures and reduced atmospheric demand.

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| Figure 1: Daily site-level environmental characteristics of a) maximum vapor pressure deficit (D) and photosynthetically active radiation (PAR) b) mean volumetric water content at 5 cm and 10 cm, total precipitation, and air temperature. Labeled boxes subdivide the study period into before, during, and after the monsoon season |

Seasonal GPP dynamics were similarly responsive to precipitation inputs (Fig. 1 b). GPP declined during the premonsoon period to near-zero levels, while the onset of the monsoon prompted sharp increases. Interestingly, while the first major pulse event was the largest single-day total (39 mm on 2021-07-27) that corresponded to almost immediate increases in , GPP rose only modestly. All three peaks in GPP during the monsoon period lagged the moisture inputs and stayed high only briefly, in contrast to (Fig. 2 a). Fall GPP averaged , about the same as initial GPP during the premonsoon period.

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| Figure 2: Time series of a) chamber and automated daily measurements of stem water potential and b) daily total gross primary productivity (GPP). Labeled boxes subdivide the study period into before, during, and after the monsoon season. Error bars represent population standard deviation |

At a coarse scale, the dynamics of hydraulic regulation can be visually estimated by plotting stem and for each season (Fig. 3). The slope appeared similar during the premonsoon and fall periods, although W and therefore stem differed substantially between the two seasons. During the monsoon period, slopes appear to shift over time, with occurring when both W and are high; the same region during the fall season has a much shallower slope.

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| Figure 3: Midday vs. predawn stem water potential in each of three seasons. Points are colored by the concurrent daily volumetric water content at 10 cm |

#### Environmental drivers and timescales of

The hydraulic regulation model (Eqn. 2 - Eqn. 5) fit the data very well (Fig. S1, observed vs. predicted = 0.920) with low bias (slope of observed vs. predicted = 0.919).

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| Figure 4: Posterior mean and 95% CI of the a) covariate effects and b) antecedent weights of covariates associated with and . Gray horizontal lines indicate the prior means, and asterisks indicate significant covariate effects |

Temporal variation in hydraulic regulation () was strongly positively associated with antecedent vapor pressure deficit (), antecedent soil water content (), and their interaction (Fig. 4 a), indicating that *J. osteosperma* became especially anisohydric under dry atmospheric conditions when soils were wet. Given its larger coefficient, was more influential on than . While the positive effect of was primarily driven by the atmospheric dryness on the same day, soil moisture up to 11 days prior was influential (Fig. 4 b). The pressure drop parameter was negatively associated with the interaction of and , although the main effects were not significant (Fig. 4 a).

#### Temporal patterns in and GPP

Although general trends in hydraulic regulation can be inferred from grouping and by season (e.g., Fig. 3), the hierarchical Bayesian model permitted combining posterior parameter distributions with environmental covariates to produce daily timeseries of predicted (e.g., Fig. 5 a), which cannot be determined empirically. During the premonsoon, *J. osteosperma* shifted between iso- and anisohydry, with values hovering near 1. But during the monsoon season, the three main pulse events precipitated peaks in that signify extreme anisohydry, with values well above 1. Finally, in the fall, *J. osteosperma* returned to isohydry, and fell below 1.

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| Figure 5: Relationship between predicted (posterior mean and 95% CI) and daily GPP shown as a) time series across three seasons, b) bivariate plots for each season, and c) Pearson’s correlation coefficient (estimate and 95% confidence interval) during monsoon season across a range of daily offsets where GPP leads |

The trends in daily correspond well to observed time-series of GPP (Fig. 5 a), particularly in the responsiveness of both and GPP to the three main pulse events. Thus, and GPP were positively correlated during the monsoon period (, Fig. 5 b), although the peak in GPP appeared to lead the the peak in . This observation was supported by the highest Pearson’s correlation between GPP and achieved at a 1-2 day offset between the two timeseries (Fig. 5 c).

#### Plant water potential relationship to GPP

The initial GPP model (Eqn. 6, Eqn. 7) also fit the data well (Fig. 6 c, observed vs. predicted = 0.733), although with some degree of bias (slope of observed vs. predicted = 0.732) such that some high GPP values were underpredicted. Comparing the GPP and NIRv time series (Fig. 6 a), the first major pulse event elicited a strong GPP response prior to any green up detected optically by NIRv, partially accounting for the underprediction of some high GPP values. Conversely, low, near-zero GPP in mid to late July was not matched by extreme lows in scaled PAR or NIRv, resulting in overprediction of low GPP values. GPP was positively associated with NIRv and the interaction between NIRv and PAR (Fig. 6 b), though PAR alone was not significantly associated with GPP.

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| Figure 6: a) Time series of daily total gross primary productivity (GPP) with scaled values of near infrared reflectance of vegetation (NIRv) and photosynthetically active radiation (PAR). Posterior mean and 95% CI of the b) covariate effects and c) predicted versus observed GPP from the first part of the GPP model (Eqn. 7, 8). Gray horizontal lines indicate the prior means, asterisks indicate significant covariate effects, error bars represent the 95% CIs, the solid diagonal is the 1:1 line, and the dashed line represents the line of best fit |

Residuals from the initial GPP model were interpreted as fluctuations in light use efficiency (LUE), follwoing the logic of the Monteith et al. (1972) framework. Three functional forms of the residual model were tested: environmental covariates with D and (Eqn. 4, Eqn. 9), soil water content with only (Eqn. 4, Eqn. 10), and predawn water potential with only (Eqn. 11). Of the three models, the predawn water potential model had the fewest effective number of parameters (), lowest posterior predictive loss (), strongest coefficient of determination (), and lowest bias (Fig. 7 b,c).

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| Figure 7: a) Time series of daily residuals from the GPP model with daily maximum VPD (), volumetric water content at 10 cm (), and site-averaged predawn water potential (), all standardized to the same scale. Posterior mean and 95% CI of the b) covariate effects and c) predicted versus observed residuals from each residual model: Env (Eqn. 4 & Eqn. 9), Soil only (Eqn. 4 & Eqn. 10), and only (Eqn. 11). Gray horizontal lines indicate the prior means, asterisks indicate significant covariate effects, error bars represent the 95% CIs, the solid diagonal is the 1:1 line, and the dashed line represents the line of best fit |

Among the GPP residual models, the predawn water potential model (Eqn. 11) fit the GPP residuals moderately well (observed vs. predicted = 0.199) while employing the fewest effective parameters and minimizing posterior predictive loss (Fig. 7 b). Combining the initial GPP model and the best-performing LUE model using predawn water potential improved the overall from 0.733 to 0.800 and the bias from 0.732 to 0.89 (Fig. 6 c, Fig. 7 c).

The strong performance of for predicting GPP residuals is likely due to their close temporal coherence (Fig. 7 a), which outperformed alone or in conjunction with (Fig. 7 b). The antecedent weights for (Fig. S2) indicated that GPP residuals lagged soil moisture by 3-5 days, but the temporally-weighted soil moisture still did not correlated as strongly with GPP residuals as did. Surprisingly, neither D nor was significantly associated with the GPP residuals in the environmental covariates model (Fig. 7 b). This is likely because D and PAR were highly correlated (Fig. 1), and the GPP residuals already accounted for PAR.

### Discussion

In this study, we set out to improve our understanding of temporal variability in plant hydraulic regulation and its relationship to ecosystem carbon uptake. We leveraged contemporaneous, high-resolution water potential and carbon flux data to compare temporal trends in daily plant water potential, hydraulic behavior, and GPP in a dryland ecosystem. First, we found that in *J. osteosperma*, hydraulic regulation varied over the growing season. Increasing anisohydricity was observed following precipitation pulses, associated with high soil moisture and high atmospheric demand. Next, we found that GPP and were most positively correlated during the monsoon season, but with different temporal trajectories following precipitation pulses. Surprisingly, although both and responded rapidly to precipitation inputs, plants achieved maximum 2-5 days after peak GPP was reached for a given moisture pulse. Together, these results hint at the intriguing possibility that extreme anisohydry can serve to maximize soil water extraction and prolong GPP pulses in dryland ecosystems. Finally, predawn water potential represented a water stress constraint on GPP better than environmental covariates such as atmospheric and soil moisture conditions. As a direct metric of water stress, plant water potential closely matched the timing of GPP variability not accounted for by light and canopy photosynthetic capacity, clarifying the promise of vegetation water stress to enhance subseasonal GPP prediction in dryland ecosystems.

#### Temporally-varying hydraulic behavior

*Juniperus* species are considered more anisohydric than co-occurring pinyon pines due to their more cavitation-resistant xylem (Linton *et al.*, 1998), higher hydraulic safety margins (Plaut *et al.*, 2012), and lower leaf water potentials (West *et al.*, 2007; Breshears *et al.*, 2009), while their categorization based on stomatal control is less conclusive (Garcia-Forner *et al.*, 2016a). Due to less vulnerable xylem in *Juniperus*, low water potentials alone do not suggest less stringent stomatal control, as they should be interpreted relative to vulnerability curve parameters such as , or the xylem pressure at 50% loss of hydraulic conductance. Here, a 166-day time series of and in *J. osteosperma* reveals strong, context-dependent variation in hydraulic regulation, an intermediate timescale that can potentially bridge the gap between short-term stomatal response-based definition of iso/anisohydry (Tardieu & Simonneau, 1998) and definitions that rely on seasonal extremes (Klein, 2014; Martı́nez-Vilalta *et al.*, 2021). We posit that using response-based metrics (Kannenberg *et al.*, 2022b) to quantify plant water use strategies can enable predictive understanding of plant-environment interactions.

Dry air in combination with wet soil drove large increases in in *J. osteosperma*, attesting to the importance of vapor pressure deficit as a driver of plant responses (Novick *et al.*, 2016; Grossiord *et al.*, 2020). As the same drivers were important for hydraulic regulation in the drought-tolerant desert shrub, *Larrea tridentata* (Guo *et al.*, 2020), transient drops in may be strategic only during the wet periods of otherwise water-limited ecosystems, when the reward of carbon uptake exceeds the risk of embolism. In our study, shifts to extreme anisohydry appeared only as responses to discrete monsoon precipitation pulses, suggesting that flexible hydraulic behavior enables *J. osteosperma* to take advantage of soil moisture when available. The responsiveness of hydraulic behavior to soil moisture may explain why, despite similar lateral root densities as pinyon pines (Schwinning *et al.*, 2020), junipers tend to be more physiologically responsive to moderate moisture inputs (Breshears *et al.*, 1997; West *et al.*, 2007; Guo *et al.*, 2018).

The positive relationship between and GPP, particularly during the monsoon season, suggests that temporally-variable hydraulic regulation can maximize carbon uptake during periods of patchy moisture availability. Most interestingly, the timing of and GPP indicates that extreme anisohydry intensifies after GPP peaks. After a precipitation pulse when soil moisture is high, GPP may be immediately stimulated, such that relatively high midday water potentials (low ) are sufficient to drive water transport along the soil-plant-atmosphere continuum. Because soil moisture declines rapidly after precipitation pulses, extreme anisohydry ( > 1) may serve to decrease midday water potentials, maintain water transport in drying soils, and possibly confer a competitive advantage over co-occurring understory species (e.g., Barron-Gafford *et al.*, 2021). The propensity of *Juniperus* spp. to extract soil water even at low soil water potentials (West *et al.*, 2007) is consistent with extreme anisohydry and prolonged elevation of GPP as soils dry.

#### Possible mechanisms of flexible hydraulic behavior

The mechanisms underlying temporally flexible hydraulic behavior are not well understood, although there are some tantalizing hints in similarly temporally-variable leaf water relations and ABA synthesis. Both *Larrea* and *Juniperus* experience seasonally varying leaf water relations and a strong difference in turgor loss point between rehydrated and un-rehydrated leaves (Meinzer *et al.*, 1986; Meinzer *et al.*, 2014). By extrapolating the pressure-volume relationships, Meinzer et al. (2014) found that turgor loss would ultimately occur at -8.2 MPa for *J. monosperma*, and indeed 99.1% of our individual observations occurred above this threshold. Seasonally varying leaf-water relations in anisohydric species may indicate that a combination of osmotic and cell wall elasticity adjustment can maintain turgor across different levels of leaf hydration.

Hydraulic regulation strategies could also be linked to temporal dynamics of foliar ABA during soil water stress and recovery (Brodribb & McAdam, 2013). In *Callatris rhomboidea*, sustained water stress led to a decline in ABA such that loss of leaf water potential (and thus guard cell turgor) drove stomatal closure, but conversely, low ABA also enabled rapid recovery after rewatering (Brodribb & McAdam, 2013). Among *Cupressaceae*, including *Juniperus* and *Callatris*, the use of leaf desiccation to close stomata during water stress (Brodribb *et al.*, 2014) could explain how *J. osteosperma* is able to tolerate dry periods and respond rapidly to rewetting events, enabling persistence in seasonally dry ecosystems.

Finally, temporal variability in plant hydraulic regulation may also be associated with the timing of belowground dynamics, such as fine root and mycorrhizal development (Peek *et al.*, 2006; Lehto & Zwiazek, 2011). In *J. osteosperma*, fine roots grew when soil water was most available and shifted toward deeper layers as the growing season progressed (Peek *et al.*, 2006), and root distributions varied depending on cool-season vs. warm-season precipitation. Rooting dynamics can directly influence plant water potential via rhizosphere conductance, but this is difficult to measure empirically (Bristow *et al.*, 1984; Sperry *et al.*, 2016). Similarly, mycorrhizal symbionts are known to alter root conductivity (Lehto & Zwiazek, 2011), enhance stomatal conductance (Augé *et al.*, 2015), and increase plant productivity (Mohan *et al.*, 2014), but the temporal dynamics of plant-mycorrhizae relationships under field conditions are poorly understood and deserve further study (Gehring *et al.*, 2017).

#### Implications for hydraulic modeling

Plant hydraulic schemes are becoming increasingly represented in vegetation and land surface models (Kennedy *et al.*, 2019b; Eller *et al.*, 2020; Sabot *et al.*, 2020). The link we observed between hydraulic strategy and GPP reinforces the value of these approaches for improved predictions of GPP, especially in dryland ecosystems where patchy resource availability leads to widespread underpredictions of both the magnitude and variability of carbon fluxes (Biederman *et al.*, 2017; MacBean *et al.*, 2021b; Barnes *et al.*, 2021). Temporal heterogeneity in plant hydraulic strategy and spatial heterogeneity in topoedaphic characteristics may also interact, as evidenced by high variance in stem among seven co-located trees Fig. 2, and contribute to model underperformance in dryland ecosystems. However, if transient anisohydry does indeed represent a life history strategy to maximize carbon uptake during pulses of moisture availability, then these models will need to allow for vegetation hydraulic strategies to vary over time.

One avenue of model development operationalizes the trade-off between carbon gain and hydraulic costs (Sperry *et al.*, 2016; Wolf *et al.*, 2016; Mencuccini *et al.*, 2019), a subset of stomatal optimization models that accounts for the cavitation risk of low plant (Wang *et al.*, 2020). The Sperry (2016) model simulated the water potential and transpiration of co-occurring *P. edulis* and *J. monosperma* with high accuracy, but did not assess temporal variation in GPP. Improving the temporal fidelity of optimization models could involve explicit implementation at multiple timescales (daily, weekly) to represent plant physiological acclimation to a changing environment (Joshi *et al.*, 2022). Promisingly, temporally-variable water use strategies may arise as an emergent property of such models (Kannenberg *et al.*, 2022b), although a deeper understanding of underlying mechanistic processes (e.g, turgor maintenance across leaf hydration gradients, ABA synthesis, belowground temporal dynamics) is needed. Broadly, more research regarding when, where, and how temporally-varying water use strategies arise is necessary to evaluate their role in improved modeling of dryland carbon fluxes.

#### Importance of plant water potential

The logic of Monteith et al. (1972) relates the meteorological constraint of available sunlight with the vegetation constraint of available leaf area, modified by the conversion efficiency of light that differs by plant types (Running *et al.*, 2004). Variability in light use efficiency (LUE) can originate from demand-side constraints, such as respiration costs that scale with plant size and habit (Hunt, 1994), or supply-side constraints, such as temperature or VPD thresholds that down regulate photosynthesis. Supply-side water limitation may be especially relevant for capturing drought impacts on GPP (Schwalm *et al.*, 2010), which tend to affect photosynthesis more than respiration. However, VPD alone is insufficient to capture drought effects, as soil moisture limitations on LUE can significantly reduce annual GPP (Stocker *et al.*, 2018), especially in dryland regions.

In our study of a single growing season, we found that predawn water potential matches the temporal pattern of LUE even more strongly than antecedent soil moisture, which comports with the critical role of water potential to plant physiology. Importantly, predawn water potential improved GPP model fit even though measurement scales varied greatly, with NIRv derived from 500 m MODIS data, GPP from a flux tower, and stand water potential averaged from 7 trees within the tower footprint, suggesting that the theoretical foundation connecting plant hydraulics to ecosystem productivity is robust to significant scale mismatch. Current initiatives to collect and aggregate soil and plant water potential in conjunction with flux tower measurements, including the Ameriflux ‘Year of Water’ and the PSInet RCN database, are anticipated to improve water potential data availability and spur new approaches to estimating vegetation water stress beyond single-site studies.

#### Conclusions

Though classically considered anisohydric, *J. osteosperma* exhibited multiple hydraulic regulation strategies within a growing season. Extreme anisohydry was only evident after monsoon precipitation pulses, while soils were rapidly drying yet carbon uptake was high. This suggests that temporally flexible hydraulic regulation allows *J. osteosperma* to both avoid extreme and xylem cavitation during seasonal drought and prolong high carbon uptake following episodic precipitation events. Evaluating plant water potential at intermediate timescales can reveal the important contribution of hydraulic regulation to the magnitude and timing of dryland ecosystem fluxes.

### Data availability

All data and code are stored in a GitHub repository that will be made public and archived on Zenodo upon manuscript acceptance.

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### Author contributions

JSG and SAK conceived of and designed study with input from WRLA. Field data were collected by SAK, processed by SAK and JSG, and analyzed by JSG. Remote sensing data were processed by MLB and analyzed by JSG with input from WKS. JSG prepared the manuscript with input from all co-authors. All authors reviewed the results and approved the final version of the manuscript.

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### Supporting Information

**Fig. S1** Model fit of

**Fig. S2** Covariates, antecedent weights, and model fit of GPP residual model with environmental covariates

**Fig. S3** Covariates, antecedent weights, and model fit of GPP residual model with soil water content

**Table S1** Model comparison statistics for the GPP residual model